
Challenges in integrative approaches to modelling the marine ecosystems of the North Atlantic: Physics to fish and coasts to ocean

Jason Holt^{a,*}, J. Icarus Allen^b, Thomas R. Anderson^c, Robert Brewin^b, Momme Butenschön^b, James Harle^a, Geir Huse^d, Patrick Lehodey^e, Christian Lindemann^f, Laurent Memery^g, Baris Salihoglu^h, Inna Senina^e, Andrew Yool^c

^a National Oceanography Centre, 6 Brownlow Street, Liverpool L3 5DA, UK

^b Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK

^c National Oceanography Centre, European Way, Southampton SO14 3ZH, UK

^d Institute of Marine Research, Nordnesgt 33, N-5085 Bergen, Norway

^e MEMMS, CLS Space Oceanog. Div, Ramonville St Agne, France

^f DTU-AQUA, National Institute of Aquatic Resources, Jægersborg Allé 1, 2920 Charlottenlund, Denmark

^g LEMAR, CNRS/UBO/IRD, Technopole Brest Iroise, 29280 Plouzané, France

^h Institute of Marine Sciences, METU, Erdemli, Mersin, Turkey

*: Corresponding author : Jason Holt, Tel.: +44 (0)1517954853 ; email address : jholt@noc.ac.uk

Abstract:

It has long been recognised that there are strong interactions and feedbacks between climate, upper ocean biogeochemistry and marine food webs, and also that food web structure and phytoplankton community distribution are important determinants of variability in carbon production and export from the euphotic zone. Numerical models provide a vital tool to explore these interactions, given their capability to investigate multiple connected components of the system and the sensitivity to multiple drivers, including potential future conditions. A major driver for ecosystem model development is the demand for quantitative tools to support ecosystem-based management initiatives. The purpose of this paper is to review approaches to the modelling of marine ecosystems with a focus on the North Atlantic Ocean and its adjacent shelf seas, and to highlight the challenges they face and suggest ways forward. We consider the state of the art in simulating oceans and shelf sea physics, planktonic and higher trophic level ecosystems, and look towards building an integrative approach with these existing tools. We note how the different approaches have evolved historically and that many of the previous obstacles to harmonisation may no longer be present. We illustrate this with examples from the on-going and planned modelling effort in the Integrative Modelling Work Package of the EURO-BASIN programme.

Highlights

► The state of the art in simulating marine physics, planktonic and higher trophic level ecosystems is reviewed. ► This is illustrated with examples from the EURO-BASIN programme, focusing on the North Atlantic and its adjacent shelf seas. ► The challenges faced are highlighted and ways forward suggested.

Introduction

The North Atlantic Ocean and its contiguous shelf seas provide a diverse range of goods (e.g. food, renewable energy, transport) and services (e.g. carbon and nutrient cycling and biodiversity) to mankind. However, global climate change will lead to substantial changes in the physical conditions of the basin (e.g. circulation, stratification, temperature and light climate). At the same time, combinations of direct anthropogenic drivers (e.g. fishing and eutrophication) impact at both an organismal and population level, thereby influencing the biogeochemical cycles of carbon and nutrients on a regional and basin wide scale. The coupling between the climate, marine ecosystems and the human impacts on these ecosystems is a key facet of the Earth System, of which our understanding is only beginning to scratch the surface. This coupling relates to two overarching scientific issues of immense societal concern:

- the role of the oceans in mitigating the effects of anthropogenic CO₂ emissions,
- the impacts of climate (change and variability) and fishing pressure on ecosystem structure and function, and the consequences for biodiversity and fisheries production.

BASIN ([Wiebe et al., 2009](#)) is a joint EU/North American research initiative with the goal of elucidating the mechanisms underlying observed changes in North

1 Atlantic ecosystems and their services, and EURO-BASIN is a programme to
2 implement this, funded under the European Commission's 7th Framework
3 Programme. Much can be learned on these issues through an extensive observational
4 and experimental effort, however, a crucial challenge for BASIN is to develop the
5 predictive capability necessary to understand the space and time variation of broadly
6 distributed and dominant members of the North Atlantic plankton and fish
7 communities, the relevant biogeochemical processes, as well as feedbacks between
8 and within these components and climate. It is only through the development and
9 application of integrative modelling that these questions can be explored together and
10 under possible future conditions, potentially far removed from any conditions in the
11 observational base. In this paper, we explore the fundamental challenges of an
12 integrative approach to modelling the marine ecosystem in the North Atlantic and its
13 adjacent shelf seas, with a focus on these overarching issues. To illustrate this, we
14 draw on examples from the Integrative Modelling Work Package in the EURO-
15 BASIN programme, where state of the art models of physical, lower and higher
16 trophic level processes are deployed. In the remainder of this introduction we set the
17 scene by considering how these two overarching issues give rise to key science
18 objectives in this region.

19 While the open-ocean (Sanders et al., This volume) and shelf seas (e.g. Chen and
20 Borges, 2009) biological carbon pumps are well established, the dynamics of these
21 processes and their vulnerability to future change are far from certain. This is
22 particularly the case in the context of changing marine management strategies and
23 physical, ecosystem and biogeochemical responses to climate change and variability.
24 The recent identification of the 'non-steady-state' nature of the ocean carbon pump
25 (e.g. in the North Atlantic: Schuster and Watson, 2007; Watson et al., 2009) and its
26 response to climate raises concerns over its ability to continue to mitigate increasing
27 atmospheric CO₂ levels (Le Quere et al., 2010).

28 Alongside the carbon cycle context, the structure and function of the ecosystem
29 itself and how this responds to changing external conditions such as climate and
30 fishing pressure is of particular importance as it relates to the economic and food
31 security aspects of the exploitation of living marine resources (Stock et al., 2011), and
32 also the societal drive to ensure a healthy marine environment. In Europe this is

1 encapsulated in the Marine Strategy Framework Directive (MSFD) and the
2 descriptors of Good Environmental Status therein¹.

3 Figure 1a shows a schematic contrasting the shelf sea and open-ocean biological
4 carbon pumps. In both cases the driver is the same, photosynthesis (P). However, the
5 pathways of the fixed carbon to the point where it is isolated from atmospheric
6 exchange on centennial time scales are very different. In the open ocean the
7 respiration (R) that occurs as material sinks is a critical control, whereas in shelf seas
8 the on/off-shelf transport is an important additional factor (Holt et al., 2009; Wakelin
9 et al., 2012). In shelf seas much of the sinking carbon enters the benthos, but it is still
10 largely respired and its long term fate largely depends on the relation between lateral
11 transport (pathways and time scales) and the exposure to atmospheric exchange
12 through vertical mixing. In both cases top-down control (grazing, G) has the potential
13 to alter these pathways. This simple conceptual model belies the underlying
14 complexity of the ecosystem (e.g. Figure 1b), whereby individual organisms compete
15 for resources at trophic levels from primary producers to top predators, leading to
16 intricate ecological interactions. While this ecology has long been studied in the
17 context of Living Marine Resources (e.g. Hardy, 1924), its relationship to the carbon
18 cycle is far from clear.

19 The North Atlantic is important and unique in several respects. It is a key
20 component in the climate system due to the substantial poleward heat flux in its
21 surface waters and the formation of intermediate/deep water masses in its northern
22 regions that help drive the Thermohaline Circulation (Macdonald and Wunsch, 1996).
23 This region accounts for 23% of the global marine sequestration of anthropogenic
24 CO₂ despite having only 15% of the area (Sabine et al., 2004). This arises because of
25 the deep winter mixing forming intermediate and mode water masses combined with a
26 lower Revelle factor than other mid- to high latitude regions. There is exceptionally
27 high primary production (for a large ocean basin area) in the sub-polar gyre region
28 (e.g. Carr et al., 2006) owing, among other factors, to significantly deeper winter
29 mixed layers than other ocean basins (de Boyer Montégut et al., 2004). The ocean
30 basin is bounded by shelf and marginal seas that support substantial economic activity

¹ <http://ec.europa.eu/environment/water/marine/ges.htm>

1 (e.g. fisheries) and are themselves bounded by populous countries of Europe and
2 Africa on the eastern side and the Americas on the west. Hence, impacts of large
3 coastal cities and resource exploitation are acutely felt in this region, potentially
4 mitigated by recent legislative action (e.g. MSFD). In contrast, the less developed
5 countries of West Africa rely on artisanal fisheries as an important protein source
6 (FAO, 2012) and so are highly vulnerable to changes in fish production in this
7 upwelling region.

8 The particular question within the BASIN programme we aim to make progress
9 towards answering are:

- 10 • What defines the biogeographic regions of the North Atlantic, and how might
11 these change, and in what way and on what time scales might the ecosystem
12 respond to these changes?
- 13 • What is the impact of top down control on the carbon cycle and phytoplankton
14 community structure, how does this vary temporally and spatially, and under
15 future climate and fisheries management scenarios?
- 16 • What are the pathways and ultimate fate of carbon sequestered by biological
17 production, and how might these change?
- 18 • How does climate change and variability impact the ecosystem productivity,
19 structure and function?

20 This requires a truly integrated modelling approach that spans from fisheries to
21 plankton, and from the shelf seas to the open ocean. However, to achieve this we must,
22 not only make significant advances in modelling individual systems, but also break
23 down barriers in traditional scientific approaches, for example between modelling
24 biogeochemical systems and modelling ecological systems, and between modelling
25 the open-ocean and coastal-ocean. There is of course sound scientific reasons why
26 different approaches are taken for each of these so full harmonisation is neither
27 possible nor desirable, but to move towards the goal of an integrative system we must
28 find the common ground and exploit the potential linkages.

29 Modelling approaches are context dependant; at each stage (physics,
30 biogeochemistry, ecosystem, etc.) there are several complimentary ways to explore
31 the system differing in how the system is represented, in the time and space scales

1 considered, and in the capability to address the particular questions at hand. Each will
2 be a compromise in some sense, but also have particular advantages. Hence an
3 integrative modelling approach needs to embrace this diversity and rather than
4 providing a single mechanistic connection between drivers, impact and response, each
5 component provides complimentary evidence towards our understanding of the
6 system's behaviour. Practical considerations inevitably limit the approach to a few
7 discrete choices.

8 Within EURO-BASIN, we consider three configurations of a common physical
9 model (Nucleus of a European Model for the Ocean, NEMO; Madec, 2008); three
10 biogeochemistry/lower trophic level (LTL) models (ERSEM, MEDUSA and PISCES,
11 described below); a regional scale Individual Based Model for the zooplankton
12 species *Calanus spp.* coupled to a small pelagic fish (herring) population (Utne et al.,
13 2012; Utne and Huse, 2012); a spatially explicit size-based model of open-ocean
14 ecosystems, which aims to represent the joint effects of environmental variability and
15 fishing on the structure and dynamics of pelagic ecosystems (APECOSM; Maury et
16 al., 2007a; Maury et al., 2007b); and a spatially explicit population dynamics model
17 (SEAPODYM; Lehodey et al., 2008; Senina et al., 2008; Sibert et al., 2012)
18 predicting the effects of environment and fishing on key pelagic species, and
19 including a functional representation of Mid Trophic Level (MTL) groups (Lehodey
20 et al., 2010) that are forage species of large oceanic predators (e.g., tuna, marine
21 mammals, seabirds). We also consider a convective scale phytoplankton IBM. The
22 particular combinations we consider here are listed in Table 1.

23 Specific issues we address in this paper are:

- 24 • Ocean physics in the open-ocean and shelf seas, and the coupling between the
25 two (section 2)
- 26 • Biogeochemistry and lower trophic level (plankton) ecosystems (section 3)
- 27 • Higher trophic levels including populations or functional groups of mid
28 trophic level (micronekton) and top predators, and the coupling between these
29 (section 4)
- 30 • Experiment design for climate change impact simulations (section 5)

31 Finally we conclude (section 6) by exploring how this approach can specifically
32 address the questions identified above.

2. State of the Art and challenges for physical models of biophysical interaction in the North Atlantic

The modelling of marine ecosystems is intimately linked to modelling marine hydrodynamics. The often quoted remark by Doney (1999) “biogeochemical models are only as good as the physical circulation framework in which they are set”, implies that we must consider which aspects of the physics are important controls of the ecosystem, how well these are modelled and how this might be improved. When considering lower trophic levels (LTLs) and biogeochemistry, there are essentially three paradigms that mediated the biophysical interactions. First is the physiological response of the organism to the environmental conditions (e.g. temperature response of growth rates; Eppley, 1972). Second, mixing and transport processes control both the phytoplankton’s exposure to light, hence triggering blooms (Chiswell, 2011; Huisman et al., 1999; Sverdrup, 1953; Taylor and Ferrari, 2011), and the resupply of nutrients to euphotic waters. These generally act on seasonal or shorter time scales and are predominantly vertical processes, but it is appropriate to include mesoscale eddy and cross-frontal transport processes here. Finally, the basin scale transport sets the overall elemental budgets, e.g. of carbon and nutrients; a simple view of this is provided by the LOICZ² methodology (Gordon et al., 1996) of fluxes into and out of a well mixed box.

The modelling of higher trophic levels is considered in more detail in section 4, however, it is worth briefly identifying some key aspects of the biophysical interactions applicable to that case. As soon as we are concerned with species, rather than ‘functional groups’ then issue of habitat arises, and whether or not it is suitable for a particular species across its life stages, depending on the behaviour of a population, time/space scale of change in the habitat and their ability to acclimate and eventually evolve to accommodate this change. This introduces other facets to the biophysical interaction that are not so important for biogeochemical/LTL considerations, namely: the ‘bioclimate envelope’ of the habitat (Cheung et al., 2009) and the connectivity and transport between regions of different habitats. i.e what is the acceptable physical environment for a species and can an individual successfully

² Land Ocean Interaction in the Coastal Zone; <http://www.loicz.org/>

1 move between regions of these characteristics as it changes life stage (and so
2 environmental preference), given that these regions are themselves changing, on
3 generally longer timescales? This then puts more detailed requirements on aspects of
4 the physics to be modelled and understood, which are not necessarily required for
5 modelling LTLs. Examples on the timing of stratification and spring blooms to
6 determine prey availability (Beaugrand et al., 2003b), and on the details of currents to
7 move larvae from spawning grounds (e.g. Petitgas et al., 2013).

8 While basin-scale oceanography and its climate variability drive the population
9 dynamics of pelagic species (Lehodey et al., 2006), the mesoscale activity is also of
10 interest to investigate in detail the behaviour of animals and to address key
11 mechanisms that need to be included in the new generation of population dynamics
12 models. Various sources of biological data exist today (e.g., fishing data, acoustic, and
13 satellite tags) that can be confronted to these multiple spatial and temporal scales
14 (Lehodey and Maury, 2010).

15 Generally, the biophysical interactions put specific requirements on a
16 hydrodynamic model used to simulate ecosystem processes, which in turn impose
17 limits on the accuracy of the ecosystem model (e.g. Sinha et al., 2010). Ecosystem
18 processes are often non-linearly dependent on material fluxes that are not constrained
19 by external feedbacks, and so maybe more sensitive to internal model dynamics than
20 aspects of the physics often used for model validation. The classic example is sea
21 surface temperature (SST) and diapycnal mixing. While SST is an important
22 parameter for coupled ocean-atmosphere modelling, successfully reproducing the
23 field (compared with the plentiful observations) is not a particularly good guide to
24 whether the mixed layer dynamics are well modelled, since the sensible heatflux will
25 compensate for errors in this. In contrast, accurately modelling mixed layer properties
26 is a necessary condition for a well modelled phytoplankton seasonal cycle; i.e. success
27 (or otherwise) in modelling the ecosystem should be used as a guide to improving the
28 physical model.

29 Horizontal resolution is crucial, and central to this is whether motions at the first
30 baroclinic Rossby radius are permitted. This allows a class of phenomena that are
31 either absent or poorly represented in coarser resolution models to be simulated,
32 specifically: coastal upwelling, mesoscale eddies and internal tides; all of which have

1 important consequences for the modelled ecosystem. The scale for many important
2 processes is the first internal Rossby radius of deformation (R_1 ; Figure 2). The eddy
3 scale (L_o) is known to vary linearly with R_1 from both empirical altimeter based
4 studies, $L_o \sim 1.7R_1 + 86\text{km}$, (Stammer and Boning, 1996), and theoretical and laboratory
5 studies ($L_o \sim \pi R_1$) such as those of Griffiths and Linden (1982). Similarly the lateral
6 scale of upwelling velocity is also, R_1 (Huthnance, 1995); this can be shown
7 analytically for the case a vertical wall, but R_1 decreases rapidly at the shelf edge so
8 resolving the deep ocean value should be seen as a lower bound. Internal tides have a
9 wavelength $\sim R_1/f/\omega$, so show a similar pattern to the Rossby radius, but without the
10 strong increase towards the equator. Internal tides and upwelling require several grid
11 cells per Rossby radius, whereas mesoscale eddies can be permitted at lower
12 resolution owing to the multiplier in their scaling. However, upwelling will still occur
13 in models that do not resolve this scale, but it will not be well represented; internal
14 tides and eddies will simply be absent. The ORCA series of global NEMO model
15 configurations includes $1/12^\circ$, $1/4^\circ$ and 1° versions, with typical grid size in the North
16 Atlantic of, respectively, 6km, 18km, and 72km. From Figure 2, the $1/12^\circ$
17 configuration can be characterised as being eddy resolving in the subtropical gyre
18 ($e = R_1/\Delta x > 4$), comfortably eddy permitting in subpolar gyre and nordic seas ($e \sim 1-4$),
19 but eddy excluding on-shelf ($e < 1$). The $1/4^\circ$ model reduces this ratio by a factor of 3
20 so is eddy permitting in sub-tropical gyre, marginally eddy permitting in sub-polar
21 gyre, otherwise eddy excluding. Alongside the dynamical scales, the resolution of
22 geographic scales (bathymetry and coastline) is important in determining the local of
23 the currents (such as the Gulf stream) and between basin transport.

24 To illustrate the importance of horizontal resolution, results are presented for three
25 models with comparable physics but different horizontal resolution in the ORCA
26 series of NEMO models, along with climatological observations, for surface current
27 speed (Figure 3), mixed layer depth (MLD; Figure 4), and sea surface temperature
28 (SST; Figure 5). Ecosystem models are, to some extent, tuned to a particular
29 representation of the physical environment, i.e. the time/space scales and process
30 representation. Ideally this would be the best physical representation available, but
31 inevitably practical considerations limit this, and ecosystem models tend to be
32 developed and tuned on the coarser end of this scale. This potentially leads to error

1 compensation and over-tuning of the ecosystem model to compensate for inadequate
2 physics (Popova et al., 2006). Hence a detailed analysis is required of how different
3 aspects of the physics are modelled and how these constrain the ecosystem.

4 **Transport processes in the North Atlantic**

5 Of the many currents forming the gyre circulations in the North Atlantic, the Gulf
6 Stream and its extension into the North Atlantic Current and Azores Current is the
7 most prominent. The currents on the eastern side (e.g. the eastern margin slope
8 current; Pingree et al., 1999; Souza et al., 2001) are weaker, but none the less form
9 important components of the circulation. The Gulf Stream path has particular
10 importance to the surface fluxes, for example Eden and Oeschler (2006) in studying
11 OCMIP-2 model biases found that “[the biases] lead to a large range of simulated
12 total air-sea carbon flux patterns and in consequence a large uncertainty in simulated
13 oceanic uptake of anthropogenic CO₂”.

14 A central issue in modelling the circulation of the North Atlantic is to achieve an
15 accurately located Gulf Stream separation at Cape Hatteras, and subsequent current
16 pathways, particularly the Northern Excursion. This has been the subject of
17 substantial effort and current thinking is that many factors, including coastline,
18 bathymetry, barotropic-baroclinic coupling with the deep western boundary current,
19 and mesoscale eddies, control this circulation (see Hecht and Smith, 2008 and
20 references therein). Similarly, many modelling factors play a role in producing a
21 realistic Gulf Stream separation. There is great sensitivity to subgrid scale
22 parameterisations, boundary conditions (or global versus regional domains) and
23 choice of dissipation operators (Chassignet and Marshall, 2008). Bryan et al (2007)
24 suggest the Gulf Stream is greatly improved as the horizontal resolution is reduced
25 below 10km, thus resolving the first baroclinic Rossby radius and also more
26 accurately representing the bathymetry and coastline. This is clearly seen in Figure 3
27 in terms of the location of the surface maximum and Figure 5 in terms of the location
28 of the temperature front. As far as numerical solution methods are concerned, Barnier
29 et al (2006) found in a 1/4° study, that by implementing partial cells for the
30 geopotential vertical coordinates, and an energy and enstrophy conserving scheme for
31 solving the momentum equation, they were able to improve the flow patterns in the
32 North Atlantic. But given all these factors, the key determinant in accurately

1 representing the circulation is model resolution. For example, Figure 3 shows the non-
2 eddy permitting model (1° ORCA), not only underestimates the strength of the Gulf
3 Stream currents by ~ 4 fold, it separates from the coast too far north and is too zonal in
4 direction. The $1/4^\circ$ ORCA substantially improves the speed, but it is only at $1/12^\circ$ that
5 its path is accurately modelled.

6 While progress has been made through subgrid scale mixing (e.g. Gent and
7 McWilliams; (1990); see below) and topographic representation (e.g. immersed and
8 porous boundary approaches; Adcroft, 2013; Tseng and Ferziger, 2003), they are far
9 from the accuracy achieved by refined resolution, and also miss many of the nuanced
10 processes such as non-local effects of eddies. Some caution is needed as increased
11 eddy activity in a model can also result in spurious enhanced diapycnal mixing
12 (Griffies et al 2000).

13 The position of the large scale currents also impacts on the relevant water mass
14 formation, overturning circulation and hence the solubility carbon pump. The model
15 intercomparison study by Treguier et al (2005) suggests the meridional overturning is
16 primarily influenced by deep overflows, while the horizontal circulation of the gyre is
17 influenced by both deep overflows and deep convection. They suggest that difference
18 in deep convection patterns in the Labrador Sea are related to differences in their
19 barotropic transport at Cape Farewell.

20 Aside from the Gulf Stream and sub-polar gyre, an important feature of the
21 circulation on the western side of the North Atlantic is the coastal current from the
22 northern Labrador shelf to Cape Hatteras (Loder and Petrie, 1998), formed by
23 freshwater from a combination of ice melt and riverine sources. While there is
24 considerable freshwater loss to the open-ocean along this path there is also evidence
25 of some continuity of flow. In contrast many of the shelf seas on the eastern side of
26 the basin lack such a strong advective component, the Norwegian coastal current
27 being a notable exception. Generally, coastal currents carry terrestrial influence (e.g.
28 freshwater, nutrients, CDOM, Alkalinity) far from their source and are an important
29 inter-basin transport mechanism e.g. linking the Baltic, via the North Sea and
30 Norwegian Sea with the Barents Sea in the Arctic. Their accurate representation,
31 particularly the lateral transport by eddies (Johannessen et al., 1989), requires the
32 resolution of the on-shelf Rossby radius and so challenges many model systems. The

1 North Atlantic Drift joins the eastern boundary slope current in the Faero-Shetland
2 channel, another region of strong eddy activity (Sherwin et al., 2006).

3 **Mesoscale and submesoscale eddies**

4 The stratified ocean is naturally full of eddies arising from baroclinic instability
5 and the inverse energy cascade (Polvani et al., 1994). The North Atlantic is a region
6 of intense eddy activity and the growth of satellite based Earth Observation,
7 particularly altimetry but also SST and ocean colour, over the last decades has lead to
8 a substantial improvement in understanding of the eddy field in the North Atlantic
9 (e.g. Ducet et al., 2000). Bryan and Smith (1998) clearly demonstrate the importance
10 of resolution in accurately reproducing this eddy field using models of 0.4° , 0.2° , 0.1°
11 resolution. However, the role of subgridscale parameterisations and numerical
12 methods is more subtle. There is a growing appreciation of the importance of the eddy
13 field in determining the physical oceanographic properties of the basin, both the mean
14 and fluctuating components, at the surface and at depth. A correct eddy field is crucial
15 in setting key features such as the Gulf Stream separation, northward penetration,
16 formation of the Azores current, the subpolar front and the general gyre circulation
17 (Hecht and Smith, 2008). Eddies play a particularly important role in mixing, for
18 example determining mixing and stratification in the Labrador sea through baroclinic,
19 baroclinic-barotropic and convective (sub-mesoscale) eddies (Chanut et al., 2008),
20 and in setting the flow of energy between the density field and the mean circulation.

21 Models of resolution that permits or resolve motions at the Rossby Radius (see
22 above) have the potential for a realistic eddy field and represent a ‘threshold to be
23 crossed’ (Hecht and Smith, 2008) in ocean modelling capability, which has now been
24 crossed in many dynamical studies. However, as is discussed further below, ocean
25 models used for biogeochemical studies, and especially those used as the ocean
26 components of an Earth Systems Model, have not generally crossed this threshold,
27 despite the well-established link between mesoscale eddies and oceanic production.
28 The computational constraints are simply too great, since the CPU costs increase as
29 $(1/\Delta X)^3$ and storage costs as $(1/\Delta X)^2$. Hence, the subgrid scale parameterisation of
30 mesoscale eddies represents an important area of research, and the North Atlantic has
31 provided the natural laboratory for this. Of particular note are the parameterisation of
32 Gent and McWilliams (GM; Gent et al., 1995) and Fox-Kemper et al (2008), which

1 attempt to account for the mean transport component of eddy flux (the “bolus
2 velocity”) and the up-gradient eddy transport (Eden, 2007). The use of GM has
3 greatly improved the physical simulations of non-eddy resolving models, but many
4 problems remain notably in the Gulf Stream Separation and the Northwards Gulf
5 Stream excursion. The impact of this on the modelled biogeography and
6 biogeochemical process in the North Atlantic has yet to be established and this is an
7 important consideration in EURO-BASIN.

8 In the case of eddy permitting models, subgrid scale parameterisation focuses on
9 the submesoscale and is largely an element of model stabilisation and tuning, with the
10 aim being to achieve both accurate statistics in the eddy field and well represented
11 mean properties. Models tend to employ combinations of Laplacian and biharmonic
12 operators (Chassignet and Garraffo, 2001; Hecht et al., 2008); however, a well
13 justified parameterisation based on submesoscale physics (e.g. Lévy et al., 2010) is
14 currently lacking.

15 Subgridscale parameterisation is a particular issue in coupled ocean-shelf models
16 since the dominant scales ($\sim h^{0.5}$) change dramatically at the shelf edge to the extent
17 that a model may change from being eddy permitting in the open-ocean to non-eddy
18 permitting on-shelf. This has two specific implications: the interpretation of results in
19 the two regimes needs to take this into account and the physical interpretation of ‘sub-
20 grid scale’ changes, and so should the parameterisation (e.g. Wakelin et al (2009) use
21 a simple depth dependent horizontal eddy diffusivity/viscosity). However, as noted
22 by Holt and James (2006), the treatment of horizontal diffusion is “one of the least
23 well-established areas of shelf-sea modelling and has received scant attention
24 compared with the extensive literature on vertical turbulent transport (see e.g.
25 Baumert et al., 2005)”.

26 **Mixing processes in the North Atlantic**

27 More than in any other ocean region the North Atlantic is characterised by its
28 diverse range of mixing regimes, which largely set the scene for its biophysical
29 interaction, and so need to be carefully considered in any model. The energetic
30 mixing/vertical transport processes include tides, wind mixing, mesoscale eddies,
31 deep winter convection, and coastal upwelling.

1 The North Atlantic is a region of exceptionally energetic tides and these are
2 amplified on the continental shelves of the North, Celtic, and Irish Seas (on the
3 eastern side of basin) and Bay of Fundy and Hudson Straits (on the west) to give the
4 largest tidal amplitudes globally. Shelf seas, e.g. North Sea and Georges Bank, show
5 patterns of well mixed and seasonally stratified waters set by the criterion of Simpson
6 and Hunter (1974). This in turn sets the benthic/pelagic recycling characteristics of
7 these seas and the balance between light and nutrient limitation. Modelling tides at a
8 basin and shelf scale is comparatively straightforward given their approximation to
9 coastal trapped waves under linear conditions (see Holt et al., In Press and references
10 therein), and basin scale tides are well established from inverse models derived from
11 satellite altimetry (Egbert et al., 1994). Tides, and other high frequency barotropic
12 waves, are generally not included in global and basin scale models, but their inclusion
13 directly or at least through a parameterisation (e.g. Simmons et al., 2004) is a
14 prerequisite for a model that aims to simulate both the open ocean and shelf sea
15 regimes. In a model with a fixed vertical grid including tides would be expected to
16 result in spurious diapycnal mixing, and hence deterioration of water mass properties.
17 Time varying vertical coordinates and a re-mapping vertical advection approach may
18 address this (James, 2000), and this approach has recently been incorporated into the
19 NEMO model.

20 A primary consideration in tidal modelling is that the benthic boundary layer is
21 well resolved. In mid- and high latitude regions the cyclonic component of the
22 boundary layer is very thin (Soulsby, 1983). Along with the need to resolve sharp
23 pycnoclines, this is one motivation for the use of terrain following coordinate models
24 in tidally active shelf seas, such as those bordering the North Atlantic. Difficulties
25 tend to arise where the boundary layer meets stratification and accurately modelling
26 the resulting sporadic diapycnal mixing (e.g. spring-neap tidal pumping; Sharples et
27 al., 2001), is problematic.

28 The Northern North Atlantic is an exceptionally windy region, comparable to the
29 northern North Pacific and Southern Ocean in annual mean wind stress (e.g. Josey et
30 al., 2002). This leads to exceptionally deep mixed layers, which can be particularly
31 challenging to model (Figure 4). While monthly mean winds stresses can provide a
32 reasonable representation of the seasonal evolution of the mixed layer depth, it is well

1 known that accurately representation of the mixed layer dynamics requires high
2 frequency atmospheric forcing, ideally resolving the inertial period ($1/f$), otherwise
3 wind stresses can be significantly underestimated and phenomena such as inertial
4 shear spiking (Rippeth et al., 2009) are not represented.

5 Vertical mixing models fall into three categories: mixed-layer parameterizations
6 (e.g. KPP; Large et al., 1994), one-equation turbulence models with a single equation
7 for turbulent kinetic energy (TKE) and prescribed mixing length (Holt and James,
8 2001; Madec, 2008); and second-moment models with a second dynamic equation for
9 some combination of TKE and mixing length (e.g. for the turbulence dissipation in k-
10 epsilon models; Umlauf and Burchard, 2005). A particular feature of the North
11 Atlantic is the deep convection in northern regions. In the first two of these categories
12 this is treated by an iterative ‘convective adjustment’ process. While this is reasonably
13 successful at modelling the mixed layer depths (Figure 4), the actual turbulence levels
14 occurring with the convection are not necessarily appropriate, particularly at the
15 surface where mixing lengths are limited by the ‘Law of the wall’ ($l \sim \kappa z$). A second-
16 moment model (e.g. Generic Length Scale; Umlauf and Burchard, 2003) does not
17 have this limitation, and so is likely to better represent critical turbulence levels
18 (Huisman et al., 1999); although it still only includes local down-gradient (diffusive)
19 turbulent transport.

20 All three classes of turbulence models have varying success in modelling mixed
21 layer depth, and given its biological importance significant effort goes into tuning the
22 model to better represent this property. This is a case where the more empirical
23 models have an advantage; the models based on turbulence theory have stronger
24 constraints on acceptable parameter values, for example the closure model of Canuto
25 et al (2001) has ‘no adjustable parameters’. While this is theoretically pleasing, it is
26 problematic in practice and tends to lead to add-on such as mixing length limiters
27 (Galperin et al., 1988; Holt and Umlauf, 2008), arising because of the essentially non-
28 isotropic nature of stratified turbulence (isotropy is an underlying assumption in the
29 formulation). The local nature of the underlying formulation is also an issue; transport
30 of turbulent properties is only treated as a simple vertical diffusion. While the non-
31 local issue could be addressed with representation of transport processes such as
32 Langmuir cells and convection, care is needed owing to a more pressing issue, namely

1 numerical diffusion. Advection schemes that are non-dispersive (i.e. positive definite)
2 are generally diffusive. This gives rise to spurious numerical vertical mixing than can
3 exceed the realistic levels of physical mixing (Burchard and Rennau, 2008); the last
4 thing many ocean models need is more vertical mixing. Hence, alongside the
5 extensive observational effort in the North Atlantic to improve the parameterisations
6 of mixed layer properties, e.g. in the UK OSMOSIS project, considerable modelling
7 effort is required to minimise numerical diffusion so as to accommodate this
8 improved knowledge, for example building on the methods of Corella and Woodward
9 (PPM; 1984) and Prather (1986).

10 While, the underlying processes determining the mixed layer depths are
11 essentially vertical, they are modified by horizontal transport to the extent that the
12 mixed layer depths are strongly sensitive to horizontal resolution (Figure 4). There is
13 a clear improvement between the $1/4^\circ$ ORCA and 1° ORCA (e.g. in NE Atlantic),
14 accepting anomalously mixed layer in the Labrador Sea in the latter. The picture is
15 further improved in the $1/12^\circ$ ORCA model.

16 **Ocean-shelf coupling**

17 The challenge of modelling ocean-shelf coupling lies in the superposition of first-
18 order changes in water depth and a range of locally specific dynamical processes
19 (Huthnance, 1995). From an ecosystem point of view coastal upwelling is the most
20 prominent process in terms of ocean-shelf coupling. While the most productive
21 eastern margin upwelling systems globally are not in this region, the West African
22 and Iberian upwelling systems make an important contribution to the basin wide
23 production (Carr et al., 2006). Again this is primarily an issue of scale. The primary
24 upwelling circulation requires the (deep ocean) first Rossby Radius to be resolved,
25 whereas the complex secondary circulation, filaments (Peliz et al., 2002) and eddy
26 effects (Gruber et al., 2011) require significantly finer resolution.

27 Internal tides provide an important mechanism for enhanced mixing at the shelf-
28 edge, which have been particularly difficult to include in coupled ocean-shelf model.
29 The difficulty arises because of spurious diapynal mixing at the steep topography.
30 Other specific numerical issues for terrain following coordinate models are horizontal
31 pressure gradient (Shchepetkin and McWilliams, 2003) and horizontal diffusion

1 (Beckers et al., 2000) calculations at the juxtaposition of sloping coordinates,
2 topography and stratification.

3 The relative strength of ocean-shelf exchange, riverine and atmospheric inputs, sets
4 the elemental inventory on-shelf. These are augmented by biogeochemical processes
5 such as denitrification and nitrogen fixation (Hydes et al., 2004). The adjustment time
6 of shelf seas to oceanic conditions depends on this ocean-shelf exchange and ranges
7 from days in narrow up-welling shelves to many years on shelves with limited
8 exchange and weak circulation (e.g. ~6 years in the Celtic Sea; Hydes et al., 2004).
9 Holt et al (2012a), in a Northeast Atlantic model simulation find reasonable
10 agreement to the steady state 'LOICZ' approach for nitrate. However, the assumption
11 of a well mixed basin behind this are called in to question when salinity is considered:
12 the observed ocean-shelf salinity difference underestimates the ocean-shelf exchange
13 by a factor of 4 compared with the values given by Huthnance et al (2009); indicating
14 much of the transport occurs without significant lateral mixing with fresher coastal
15 water.

16 **Modelling North Atlantic Physics: Coast to Ocean**

17 Open-ocean and coastal-ocean hydrodynamic models have had a somewhat
18 different evolutionary history, resulting from the different scales and classes of
19 problems in the two regimes. Coastal-ocean models have focused on the requirement
20 of the vertical coordinate systems to resolve the benthic boundary layer, a free surface
21 calculation that can accommodate large amplitude waves, turbulence models capable
22 of simulating multiple boundary layers and the need for accurate open boundary
23 conditions, notable examples in the North Atlantic context are: the ~1.8km
24 POLCOMS European shelf model of Holt and Proctor (2008) and the multiscale
25 FVCOM model developed for US GLOBEC (Chen et al., 2007). In contrast, open-
26 ocean models have focused on the need to preserve water masses during long
27 integrations, the representation of meso-scale eddies (resolved or parameterised), and
28 horizontal coordinate systems on the sphere. These include both regional models such
29 those used in the DYNAMO project (Willebrand et al., 2001) and the NATL12 North
30 Atlantic Model (Treguier et al., 2012), and global models where the focus of analysis
31 has been the North Atlantic (see Hecht and Smith, 2008).

1 The choice of horizontal and vertical resolution remains a key determinant of
2 model quality and also of computational and data handling costs. At the basin wide
3 scale a clear improvement in eddy kinetic energy and Gulf Stream path has been
4 demonstrated as grids are refined. However, the models we consider here are far from
5 convergence, i.e. reaching the aspirational condition of computational fluid dynamics
6 that the solution is no longer dependent on grid resolution or subgrid scale
7 parameterisation. Those studies that have hinted at convergence (Hecht and Smith,
8 2008) have a substantially fine resolution than considered here.

9 In the shelf sea context a systematic comparison of 9 models covering (at least)
10 the North Sea with common forcing do not show a clear improvement with resolution
11 (from ~3km to 20km) when compared with temperature and salinity observation from
12 the ICES data base (Delhez et al., 2004). The introduction of stochastic properties into
13 the model and the nature of the data (point profiles) means increasing resolution does
14 not necessarily improve such model-data comparisons. Whether it leads to a ‘better’
15 model therefore depends on the questions being asked of the model, and requires a
16 more detailed investigation.

17 Global and basin scale models are now routinely run at resolutions similar to
18 historical shelf sea models (~10's km; e.g. Backhaus and Hainbucher, 1987), and so
19 are capable of representing (albeit crudely) on-shelf processes given appropriate
20 process formulation. Similarly, larger area shelf sea models are now run nested within
21 global models to investigate ocean-shelf coupling (Holt et al., 2012a) and basin scale
22 response (Chaudhuri et al., 2011); and indeed their inadequacies in deep ocean
23 regions are becoming more apparent (Holt et al., 2012b). Hence, it is now appropriate
24 to look to a unified ocean-shelf modelling system and to blur the distinction between
25 the two. The scientific benefits of this are to remove the uncertainties associated with
26 open-boundaries and to allow two-way exchange of information and material. The
27 NEMO model system (Madec, 2008) provides the opportunity for such an approach,
28 owing to its recent developments for shelf sea applications (Maraldi et al., 2012;
29 O’Dea et al., 2012). The practical benefits are through working with a common code
30 structure, traceability between open-ocean and shelf sea model characteristics, and
31 through the exchange of ideas between the two scientific communities. These benefits
32 are inevitably offset by the challenges of unified modelling of two distinct marine

1 environments that largely lead to the distinct evolution of ocean and shelf sea
2 modelling in the first place. Simply having the modelling capability in place in a
3 single system is not sufficient to address the ocean-shelf coupling issue. Moreover,
4 computational issues (CPU and data volume) still lend significant benefits to small
5 area regional models, where these are sufficient for the problem at hand.

6 **Physical Modelling in EURO-BASIN**

7 We work with three configurations at two scales: $1/4^\circ$ Global and North Atlantic
8 and $1/12^\circ$ Northern North Atlantic. The results above (Figures 3, 4, 5) show
9 significant improvement as resolution is increased and the focus of much of the
10 modelling in EURO-BASIN will be a common $1/4^\circ$ North Atlantic configuration
11 based on NATL025 (Levier et al., 2007); i.e. with significantly improved physics over
12 the 1° model. However, while this configuration approaches the 'resolution threshold'
13 identified above it does not cross it. Hence, novel physical model development in
14 EURO-BASIN focuses largely on the development of a $1/12^\circ$ Northern North Atlantic
15 Model (NNAM) building on the ORCA083 NEMO configuration. This model will be
16 used coupled to the European Regional Seas Ecosystem Model (ERSEM) and able to
17 explore the effects of crossing this threshold on biogeochemical processes and
18 biogeography of the North Atlantic at Basin scales and with realistic forcing.

19 Our starting point for NNAM is an extraction from global model spanning the
20 North Atlantic 25°N to 70°N chosen to encompass the sub-polar gyre and a large part
21 of the sub tropical gyre. Particularly, the Gulf Stream initiation provides a well posed
22 south-western boundary condition. This model is initially configured in an identical
23 fashion to ORCA083 apart from the use of lateral boundary conditions. Data for these
24 are taken from the ORCA083 model. We then incrementally incorporate features
25 appropriate to the improved representation of coastal seas, which are now described.

26 The representation of the vertical dimension is a contentious issue across all of
27 ocean modelling (Willebrand et al., 2001) and one we specifically consider in EURO-
28 BASIN, particularly in relation to ocean-shelf coupling. Geopotential coordinates are
29 the mainstay of open-ocean models, but the refinement of these through partial steps
30 (Barnier et al., 2006) and shaved cells (Adcroft et al., 1997) to better represent the
31 bathymetry and barotropic modes is an important development. In EURO-BASIN we
32 exploit the generalised vertical coordinate system in NEMO to explore the use of

1 hybrid terrain following- geopotential coordinates to gain the advantages of both in a
2 basin scale model spanning the deep ocean to the coast.

3 Tidal dynamics both from gravitational forcing and open boundary conditions will
4 be implemented, following the NW European shelf application of NEMO (O’Dea et
5 al., 2012), along with the Generic Length Scale turbulence model (GLS; Umlauf and
6 Burchard, 2003) with the parameters suggested by Holt and Umlauf (2008). The
7 ERSEM ecosystem model will be forced by river and atmospheric nutrient inputs and
8 inherent optical property specification following Wakelin et al (2012). This will
9 realise a fine resolution hybrid ocean-shelf model of the northern North Atlantic
10 clearly traceable to state of the art ocean and shelf sea models. This will allow us to
11 explore the impact of the many resolution dependent issues on the ecosystem.

12 Figure 6 shows an early stage in this process - a section across the eastern North
13 Atlantic at 51°N, for the global and regional 1/12° models differing only in that the
14 latter uses the GLS turbulence model and is forced by boundary conditions from the
15 former. This demonstrates an improved thermocline depth and thickness using the
16 GLS model and corresponding parameters. A further detailed investigation is required
17 on the implications of this scheme particularly in the context of deep winter mixing
18 and seasonality in tidally mixed waters, and whether it degrades other aspects of the
19 solution.

20 **3. State of the art and challenges for biogeochemical** 21 **and lower trophic level models of the North Atlantic**

22 The overarching concept of BASIN requires the investigation of the
23 biogeochemistry of both shelf seas and the open ocean along with the connections
24 between them at the scale of the whole North Atlantic. Alongside temperature and
25 currents, primary production at the base of the food web, zooplankton as a food
26 sources for fish and dissolved oxygen concentration (O_2) are important properties that
27 need to be realistically simulated to drive higher trophic level models. A key question
28 is how will climate variability and change, and its consequences, influence the
29 seasonal cycle of primary productivity, O_2 , trophic interactions, and fluxes of carbon
30 to the benthos and the deep ocean? Representing biogeochemistry and ecosystems in
31 ocean General Circulation Models (GCMs) and shelf sea models remains an ongoing

1 challenge given the complexity and diversity seen in marine systems. Nowhere is this
2 more the case than in the North Atlantic, with its seasonal mid- to high latitude
3 regimes characterised by ‘boom and bust’ spring bloom dynamics, and oligotrophic
4 subtropical gyres dominated by microbes. The basin is surrounded by diverse
5 marginal regions and shelf seas. These include eastern boundary upwelling regions,
6 regions strongly influenced by western boundary current intensification (and hence
7 mesoscale eddy activity impinging on-shelf), broad tidally active shelves (with strong
8 benthic-pelagic coupling), polar seas where seasonal ice cover dominates the
9 biogeochemical cycles, and regions dominated by riverine inputs and coastal current,
10 where terrestrial inputs of nutrient and CDOM play an important role.

11 Historically in a similar fashion to the physical modelling community, the open
12 ocean biogeochemical and shelf seas ecosystem modelling communities have
13 developed independently focused around different goals, but are now starting to
14 converge. Driven initially by the international JGOFS program (Hansen et al., 1999)
15 and more recently the climate change agenda, the open ocean modelling has primarily
16 focused on biophysical interactions and the quantification of the biological carbon
17 pump (e.g. Aumont et al., 2003; Fasham et al., 1990; Sarmiento et al., 1993; Yool et
18 al., 2011). At the same time, the shelf seas modellers were developing models with an
19 initial focus on nutrient cycling and eutrophication in the coastal zone (e.g. (Allen et
20 al., 2001; Franks and Chen, 1996; Schrum et al., 2006; Skogen et al., 1995; Tett et al.,
21 1994). Alongside this, the European Regional Seas Ecosystem Model (ERSEM) was
22 being developed as, what in today’s jargon is termed, an ‘end to end’ model for the
23 North Sea (Baretta et al., 1995), originally representing a foodweb that included
24 plankton, benthic fauna and fish.

25 Underlying all these models is a commonality of approach in that all the biological
26 components have been aggregated and abstracted into functional groups, which
27 represent the ecosystem in terms of pools of elemental mass, rather than individual
28 organisms or species. Marine ecosystems are complex non-linearly connected systems
29 with emergent behaviour that is not simply a function of their physical environment.
30 Hence, an ecosystem model should ideally have sufficient ecological flexibility to
31 allow this behaviour to manifest (e.g. to permit the key competitions for resources in
32 the system). In all the models considered here the trophic connections (i.e. the

1 foodweb) are fixed and the interactions are defined with fixed but uncertain
2 parameters, which are strongly dependent on the definition of the functional groups.
3 The models produce trophic interactions that adapt to their physical environment by
4 channelling mass through different components of the model ecosystem, but are
5 limited by the inability of a fixed foodweb to self-organise.

6 The first attempt to meet the challenge of modelling basin-scale ecosystem
7 dynamics in the North Atlantic using an explicit ecosystem model in combination
8 with a GCM was carried out 20 years ago by Sarmiento et al. (1993). Using a NPZD
9 model Fasham et al. (1990) coupled to a 2° resolution GCM, comparison of predicted
10 phytoplankton with satellite-derived chlorophyll showed "excellent agreement ... in
11 terms of basin scale pattern", (Sarmiento et al., 1993). Results highlighted how
12 physical forcing drives spatial patterns in marine ecosystems, as had been previously
13 demonstrated in regional modelling studies (Hofmann, 1988; Walsh et al., 1988;
14 Wroblewski, 1977). This early work supports the paradigm of biophysical interaction
15 through physical controls of nutrient resupply, in this case by seasonally varying
16 mixing and upwelling. Nevertheless, there were problems, including the timing and
17 magnitude of the spring bloom in northern latitudes, phytoplankton concentrations an
18 order of magnitude too low in the subtropical gyre and too high in the equatorial
19 upwelling region. The authors attributed most of these model-data mismatches to
20 problems associated with the physics of the GCM, and hence the focus in section 2.
21 The importance of the ecosystem representation was, however, also acknowledged. In
22 an accompanying paper in which a detailed analysis of the GCM results for Bermuda
23 station "S" was carried out, (Fasham et al., 1993) noted the critical importance of the
24 zooplankton in understanding ecosystem dynamics and of the need for observational
25 data to underpin the associated parameterisations. All of these issues still persist with
26 today's models, in spite of higher resolution physics, more complex foodweb
27 descriptions and improved parameterisations based on better understanding of the
28 underlying processes. We explore below how biogeochemical modelling of the North
29 Atlantic has progressed since this pioneering work, and what the new challenges are,
30 given the need for an integrated approach that permits prediction of both lower
31 trophic levels and associated biogeochemistry, and transfer to high trophic levels such
32 as fish.

1 **The physical controls**

2 Despite increases in the computing power during the last 20 years, most basin- or
3 global-scale GCMs that incorporate biogeochemistry are still run at a resolution of
4 $\sim 1^\circ$; this is particularly apparent in the array of Earth Systems Models used in the
5 CMIP5 process (Taylor et al., 2012). Most regional shelf seas applications are runs at
6 scales of order $1/10^\circ$, .i.e. an equivalent physical representation to 1° between 4000m
7 and 40m given that the Rossby radii crudely scale with $\sim H^{0.5}$. Hence, many of the
8 problems whereby biogeochemical predictions are compromised by model physics
9 remain, notably excess chlorophyll in equatorial upwelling areas, too low production
10 in the oligotrophic gyres (e.g. Yool et al., 2011) and in the shelf seas timing (to early)
11 and depth of stratification (to shallow; Holt et al., 2005). While, the paradigm that
12 stratification controls nutrient supply and hence phytoplankton production generally
13 holds on seasonal timescales, it breaks down on inter annual timescales in that there is
14 ‘at most a weak correlative relationship’ between inter annual variability in upper
15 ocean stratification and primary production in the subtropical gyre of the North
16 Atlantic (Lozier et al., 2011). It is not sufficient to just consider the barrier preventing
17 nutrient resupply, the processes driving this must also be considered, namely the wind
18 and buoyancy driven mixing and lateral transport.

19 Given the importance placed on mesoscale features in the physics of the North
20 Atlantic (as discussed above), one obvious solution is to increase the grid resolution.
21 The importance of mesoscale physics (e.g. eddies and upwelling filaments) in
22 controlling new production and associated biogeochemistry is well-known (e.g.
23 Gruber et al., 2011; Levy et al., 2012; McGillicuddy Jr. et al., 1998). Oschlies and
24 Garçon (2000) used a $1/3^\circ$ North Atlantic GCM in combination with an NPZD model
25 and found that, despite representing eddy-induced enhancement, primary production
26 remained too low in the subtropical gyre. It is possible to go yet further, as it is known
27 that submesoscale vertical motions can have profound effects on the structure and
28 function of plankton ecosystems (Allen et al., 2005; Allen et al., 2004; Perruche et al.,
29 2011). Increasing resolution to represent submesoscale physics, Lévy et al (2010)
30 used a $1/54^\circ$ circulation model to study gyre circulation in a closed rectangular section
31 of the North Atlantic. A strongly turbulent eddy field emerged that significantly
32 affected the overall circulation pattern. Furthermore, Lévy et al. (2012) show that

1 local increased phytoplankton growth induced by vertical sub-mesoscale dynamics
2 can be compensated by large scale effects on the thermocline and nutricline depths
3 (e.g. nutrient vertical profiles) resulting from non linear scale interactions. In this case
4 the phytoplankton production is in fact decreased in the sub polar gyre (due to
5 shallower MLD and higher zooplankton grazing) and sub tropical gyres (due to
6 deeper MLD and lower regenerated production). Shelf sea simulations that permit
7 eddies are rare, and when they have been conducted tend to be of limited area and
8 duration (e.g. Holt et al., 2004). While mesoscale eddies are commonly found in shelf
9 seas (Badin et al., 2009), their role and prevalence is less clear in these regions than in
10 the open ocean, particularly away from fronts. This arises from a limited
11 observational base, particularly as remote sensed methods (altimetry and SST) are less
12 effective in this case. Again computational restrictions prevent the routine use of eddy
13 permitting/resolving resolutions and we must turn to subgrid scale parameterisations,
14 for example of submesoscale physics, in an attempt to represent these processes in
15 both the open ocean and shelf sea contexts.

16 Beyond improved resolution and eddy processes, it is also necessary to realistically
17 parameterise vertical mixing and the associated boundary layer dynamics (i.e. surface
18 and benthic boundary layers and the pycnocline). For example, the timing and
19 amplitude of the spring phytoplankton bloom, which is such a characteristic feature of
20 the northern North Atlantic, is sensitive to wind in the late winter/early spring (Taylor
21 et al., 2002). The largest blooms are seen under conditions of decreased storm
22 intensity, which give rise to an early stratification of the water column and favourable
23 light and nutrients for phytoplankton growth (Henson et al., 2006; Waniek, 2003).
24 Accurate representation of synoptic scale atmospheric variability is required in order
25 to simulate short-term variability in physics, which may help not only in predicting
26 bloom dynamics but also other features such as realistic levels of primary production
27 in the subtropical gyres (Popova et al., 2006) and the timing of the spring bloom in
28 shelf seas. Alongside the forcing, the vertical mixing processes themselves must be
29 accurately modelled, for example to accurately simulate production in the 'deep
30 chlorophyll maximum'. While there has been substantial progress in turbulence
31 modelling (e.g. Umlauf and Burchard, 2005) accurately modelling mixing in strongly

1 stratified condition remains a challenge owing to its episodic (e.g. shear spiking) and
2 non-local (e.g. Langmuir cells) nature.

3 A process that is particularly difficult to parameterisation, and yet critical in the
4 northern North Atlantic, is deep convection. Deep convection shows strong inter
5 annual variability (Dickson et al., 2003). It has been suggested that deep convection
6 can sustain a viable phytoplankton population within the convective mixed layer
7 during winter (Backhaus et al., 2003), a supposition that is supported by model studies
8 (D' Asaro, 2008; Wehde et al., 2001) and observations (Pérez et al., 2005; Ward and
9 Waniek, 2007). Even though the water column within the deep mixed layer is general
10 homogeneous, the variable nature of deep convection can introduce heterogeneity on
11 shorter timescales. While the retraction of the mixed layer between two periods of
12 deep convective mixing may take days, primary production can react much more
13 quickly and lead to small localized blooms in the absence of stratification, prior to the
14 deep mixing re-homogenizing the water column.

15 Process studies, using a 2D (vertical-horizontal) non-hydrostatic convection model
16 coupled to a simple phytoplankton IBM have indicated that indeed low concentration
17 of viable phytoplankton can be sustained in a convective regime with local short-lived
18 growth events (Figure 7). These process studies further indicated that, while the
19 reduction in mixing depth towards spring leads to the expected increase in surface
20 phytoplankton concentration, the mixed layer integrated biomass does not increase, as
21 the higher concentration is compensated by the reduction in volume (Figure 7). A
22 comparable picture was found by Backhaus et al. (2003) at station M (66° N, 2° E),
23 who measured winter chlorophyll in 1999 (108 mg chl a m⁻²) of the same order of
24 magnitude to that of the spring bloom in 1997 (130 mg chl a m⁻²) (Irigoién et al., 1998).
25 These findings point towards a potentially underestimated pool in the carbon budget
26 that, being driven by submesoscale phenomena, is not well represented in basin-scale
27 ecosystem models. To capture the winter phytoplankton dynamics and to improve the
28 predictions of spring bloom onset, process-based parameterizations (related to
29 turbulent mixing) rather than state-based (related to mixed layer depth)
30 parameterizations could provide a way forward. In this context, net surface heat flux,
31 commonly used to estimate conditions of deep convection, has consequentially been

1 proposed to serve as a better indicator for phytoplankton growth conditions(Taylor
2 and Ferrari, 2011) than the mixed layer depth.

3 Sensitivity of ecosystem dynamics to model physics may be particularly acute for
4 complex models, e.g. those that incorporate multiple plankton function types (PFTs).
5 Sinha et al. (2010) implemented one such model, PlankTOM5.2 (which includes
6 mixed phytoplankton, diatoms and coccolithophores PFTs), separately into two 1°
7 global GCMs, with identical ecosystem parameterisations and forcing in each case.
8 Although globally integrated bulk properties, such as primary production and
9 chlorophyll biomass, were similar, predicted distributions of individual PFTs varied
10 markedly between the two simulations. Regarding the North Atlantic, relatively high
11 mixing in one GCM led to dominance by diatoms, whereas a mixed phytoplankton
12 community prevailed in the other GCM. The results highlighted that complicated
13 models have more degrees of freedom, and so a greater variety of response to
14 environmental conditions. A particular challenge then is how to assess the skill of the
15 biogeochemical model independently of the physics. It is quite possible that
16 inadequate physics is masking the skill of the biogeochemical models. One way
17 forward is the retrospective analysis of large data sets to determine robust
18 relationships between biogeochemical or ecological parameters, for example the
19 robust empirical relationships between chlorophyll concentration and phytoplankton
20 size classes (Brewin et al., 2010a; Hirata et al., 2011).

21 **Phytoplankton**

22 Phytoplankton lie at the heart of the marine biogeochemical system and the
23 challenge of modelling such systems; they drive the transformation of C, N, P, Si and
24 Fe from inorganic to organic forms, resulting in the decoupling of the carbon and
25 nutrient cycles via heterotrophic biological activity and remineralisation processes.
26 Changes in phytoplankton community composition alter the carbon (and nutrient)
27 pathways through the food web. The community structure also dictates the magnitude
28 of the vertical flux of organic material to the mesopelagic and benthos, its structure
29 and stoichiometric composition. Consequently the inclusion of multiple
30 phytoplankton PFTs such as diatoms, coccolithophores and picoplankton is an
31 obvious choice for modelling the diversity associated with the North Atlantic
32 ecosystem. Splitting phytoplankton between diatoms and non-diatoms is a common

1 strategy. Diatoms dominate the spring bloom of northerly latitudes in the North
2 Atlantic and can lead to substantial particle export that is transferred efficiently
3 through the mesopelagic zone (Martin et al., 2011). This phytoplankton group also
4 provides food for mesozooplankton, which are in turn linked to higher trophic levels
5 such as fish. Fortunately for modellers, diatoms are the one phytoplankton type which
6 is relatively straightforward to parameterise in models because, uniquely, they utilise
7 silicate for growth. The characteristic spring diatom bloom in the North Atlantic has
8 therefore been, by and large, successfully reproduced in biogeochemical GCMs and
9 shelf seas models (e.g. Lewis et al., 2006; Yool et al., 2011). The details of amplitude,
10 timing, and duration remain problematic to model as they are sensitive to the detailed
11 juxtaposition of mixing and light.

12 However, matters are considerably less straightforward when it comes to
13 accurately simulating other phytoplankton groups. A case in point is the
14 coccolithophores. Blooms of *Emiliania huxleyi* occur seasonally in the northern North
15 Atlantic (Broerse et al., 2000; Holligan et al., 1993), appearing as milky seas on
16 satellite images of ocean colour. These organisms flourish during high turbulence in
17 the early stages of the spring succession, as well as during the stratified conditions
18 that follow the spring bloom (Schiebel et al., 2011). Blooms of calcifying plankton
19 (mainly Coccolithophores) can have significant impact on Total Alkalinity (Harlay et
20 al., 2010) and air-sea fluxes (Shutler et al., 2012).

21 Using a parameterisation in which coccolithophores compete effectively at low
22 nutrients, Le Quéré et al. (2005) predicted coccolithophore blooms too far south in the
23 North Atlantic. They concluded that an improved theoretical understanding is needed
24 of the biogeochemical processes driving the growth and fate of PFTs in the ocean.
25 Gregg and Casey (2007) used a global GCM to successfully reproduce
26 coccolithophores distributions in the North Atlantic, although not in the North Pacific,
27 where coccolithophores competed successfully with other phytoplankton when both
28 nutrients and light levels were low. They concluded that "divergence among models
29 and satellites is common for such an emerging field of research". The
30 coccolithophores example is illustrative of an ongoing tension in ecological modelling,
31 namely the *a priori* requirement to increase complexity in order to achieve realism
32 versus the need to acknowledge the unwelcome ramifications of complexity, which

1 can impact the predictive skill of models. Difficulties include poorly understood
2 ecology, lack of data, aggregating diversity within functional groups into meaningful
3 state variables and constants, and sensitivity of output to the parameterisations in
4 question and their physical and chemical environment (Anderson, 2005).

5 The computational cost of increasing biological complexity generally varies
6 linearly with the number of state variables, compared with the cubic increase
7 associated with refining resolution. Hence this is a secondary consideration compared
8 to whether there is a demonstrable improvement in predictive skill and also whether
9 the overhead in making scientific interpretations of more complex models is
10 acceptable. An increase in complexity would generally be considered worthwhile if
11 accompanied by a demonstrable and unambiguous improvement in model skill.
12 However, such demonstrations are elusive and there is, as yet, no consensus as to how
13 many PFTs are required to represent key processes. Hence, flexibility in approach is
14 needed in order to select appropriate levels of complexity, depending on the question,
15 geographical area, and research agenda. This suggests the construction of model
16 frameworks in which models of different complexity can be compared in a traceable
17 fashion is highly desirable.

18 **Zooplankton**

19 Zooplankton play a pivotal role in the marine pelagic ecosystem, yet representing
20 them in 3-D biogeochemical models (as distinct from the species specific or
21 ecological models considered below) remains a major challenge (Carlotti and Poggiale,
22 2010). The most obvious division to make is between micro- and mesozooplankton,
23 both groups being important in the North Atlantic. Microzooplankton may be
24 responsible for consuming as much as half of the primary production in areas of the
25 northern North Atlantic such as the Irminger Sea and the UK coastal waters and
26 should therefore "be carefully parameterised in models of this region" (Burkill et al.,
27 1987; Montagnes et al., 2010). Mesozooplankton, and especially copepods of the
28 genus *Calanus*, are central to food web dynamics of the North Atlantic, impacting on
29 both the biological carbon pump and transfer to higher trophic levels (e.g. Beaugrand,
30 2009; Beaugrand et al., 2003a). Given the enormous disparity between micro- and
31 mesozooplankton in terms of rates of feeding, growth and reproduction, as well as in
32 life history strategies, it is highly questionable whether, as in many NPZD models,

1 they can be meaningfully aggregated into a single zooplankton state variable (e.g.
2 Popova et al., 2006).

3 Many aspects of the parameterisation of zooplankton in biogeochemical models
4 are in need of attention including functional response formulations to describe grazing
5 (Gentleman et al., 2003), stoichiometric aspects of nutrition and trophic transfer
6 (Hessen and Anderson, 2008), mortality terms (Ohman et al., 2004), and vertical
7 migration with its potential impact on carbon export (Hernandez-Leon et al., 2001;
8 Steinberg et al., 2002). One aspect of the zooplankton parameterisation that is of
9 particular relevance to the North Atlantic is the formulation of nutrient excretion.
10 When specified as a linear function of zooplankton biomass, (e.g. Aumont et al.,
11 2003; Fasham et al., 1990), this may lead to unrealistically low rates of nutrient
12 remineralisation via grazers. This problem is felt most acutely in the oligotrophic
13 gyres in GCMs and, in conjunction with issues related to model physics (above), leads
14 to extremely low predicted primary production in these areas. Significant
15 improvement in the prediction of primary production can be made if excretion is
16 instead described as a function of intake, rather than biomass (Baretta-Bekker et al.,
17 1997; Oschlies et al., 2000; Popova et al., 2006). However, partitioning the excretion
18 between DOM and POM remains a challenge. All in all, modelling zooplankton
19 represents a major challenge for the future, especially in end to end models where
20 these organisms are important both as consumers of primary production and as prey
21 for higher trophic level organisms. While single life-stage models of zooplankton are
22 probably adequate for biogeochemical cycling, this is not generally the case when
23 coupling to higher trophic levels (Rose et al., 2010). In which case consideration
24 multiple life stages is needed, and this is increasingly studied in detail using
25 individual based models (IBMs); as is discussed below.

26 **Key biogeochemical processes**

27 One of the biggest challenges is the representation of the remineralisation
28 processes in biogeochemical models specifically, the microbial loop including
29 dissolved organic matter (DOM), remineralisation of export in the deep ocean, and
30 benthic biogeochemistry in the shelf seas. The production and remineralisation of
31 particle export production in the deep ocean is discussed in detail in (Sanders et al.,
32 This volume) so it not discussed here. The microbial loop is particularly important,

1 especially in oligotrophic gyres and seasonally stratified shelf seas. It encompasses a
2 range of, largely bacterially driven, processes, leading to the remineralisation of
3 dissolved and particulate organic matter supplying nutrients to the euphotic zone to
4 drive regenerated primary production. The dissolved component is by far the largest
5 pool of organic matter in the sea. In the past DOM has been regarded as a large inert
6 reservoir of carbon, which does not have a strong effect on the export flux of carbon
7 and, below the oceans' mixed layer, is excluded from the present day carbon cycle.
8 However, from the first fieldwork in the JGOFS program (Ducklow et al., 1995)
9 studies have revealed that DOM is an active and highly dynamic component of carbon
10 biogeochemical cycles and plays important roles in marine ecosystems (Carlson et al.,
11 2010); its contribution to the total export towards the deep ocean can reach 20%.

12 However, modelling DOM has always been problematic because of the many
13 processes associated with its production and fate, as well as the fact that it has varying
14 composition and lability (Christian and Anderson, 2002; Goldberg et al., 2010).
15 Currently there are three main types of representation of microbial loop processes in
16 models. The simplest is the implicit remineralisation form, whereby POM is directly
17 re-mineralised to bioavailable nutrients according to a prescribed rate (e.g. MEDUSA;
18 Yool et al., 2011). The semi-implicit form includes those models that represent both
19 DOM and POM, but bacteria are implicit in the DOM pool. For example, PISCES
20 (Aumont et al., 2003) considers semi-labile DOM and particles of two size classes
21 (distinguished by settling velocity). This model provides multiple pathways and hence
22 timescales for nutrient regeneration. Finally, the fully explicit model whereby bacteria
23 is described along with POM and DOM, and bacteria are allow to compete with
24 phytoplankton for nutrients (e.g. ERSEM; Polimene et al., 2006; Vichi et al., 2007).
25 The choice microbial loop representation is function of the questions being asked by
26 the models. Both MEDUSA and PISCES were designed to quantify the global ocean
27 carbon cycle in both the global ocean and an earth systems modelling context, and
28 thus require a relatively simple, computationally cheap representation. On the other
29 hand if we wish to explore the ecological and biogeochemical consequences of
30 microbial processes then we need to explicitly resolve bacteria in the model (e.g.
31 ERSEM).

1 Several modelling studies (e.g. Anderson and Williams, 1998; Vallino, 2000) have
2 suggested that inclusion of DON cycling can have important implications on the
3 regulation of nutrient cycling. Salihoglu et al (2008) showed that a missing bacteria
4 component in the model can result in an important discrepancy between model and
5 observations, specifically the simulated DON pool being too high during the period
6 following the spring bloom, mainly due to the conversion of particulate organic
7 matter to DON. Even the models that include bacteria compartments predict a strong
8 annual DON cycle (Anderson and Pondaven, 2003; Hood et al., 2001; Spitz et al.,
9 2001). This suggests that the remineralization or the uptake kinetics of DON (or both)
10 are not correctly represented and need to be re-evaluated as more observations
11 become available.

12 Benthic processes and the resulting benthic-pelagic fluxes are highly significant in
13 shelf seas. Modelling studies have calculated that benthic-pelagic fluxes of nitrogen
14 and phosphorus contribute to 33% and 35% respectively to the total nutrient budget
15 on the northwest European Shelf and these compare well with observations (Proctor
16 et al., 2003; and references therein). Many physical processes influence benthic-
17 pelagic exchange. Particulate material, settling from the water column, can
18 accumulate in an unconsolidated fluff layer, which is easily remobilised by bottom
19 currents. Dissolved material is exchanged by diffusive processes in cohesive and non-
20 cohesive sediments, whereas both dissolved and particulate material is exchanged by
21 advective transport within non-cohesive sediments. All these processes are spatially
22 dependent on sediment type and hydrodynamics (including surface waves), and affect
23 the biogeochemical functioning of the benthic system. The extent to which they
24 influence shelf-wide nutrient and carbon budgets is largely unknown. Currently there
25 are two main approaches to modelling benthic processes. The first is a simple first
26 order remineralisation of the detritus reaching the seabed to define a benthic nutrient
27 flux. The second involves explicit models of benthic biota (Blackford, 1997; Ebenhoh
28 et al., 1995) and benthic nutrient cycling, (Billen and Lancelot, 1988; Ruardij and
29 Vanraaphorst, 1995), which have been developed for temperate European coastal
30 waters. This has led to the development of coupled benthic-pelagic models, whereby
31 the role of benthic nutrient cycling in controlling pelagic ecosystem dynamics can be
32 explored (Allen et al., 2001; Holt et al., 2012a). From a modellers perspective the

1 benthic system is severely under-sampled and the benthic models suffer from a basic
2 lack of information on even the seasonal cycles of the ecology and biogeochemical
3 processes. While this knowledge gap is beginning to be addressed, this is the major
4 limitation to benthic model evaluation and future development.

5 **Future developments in biogeochemical and LTL modelling**

6 Modelling biogeochemical cycling in the ocean is a complex business and a
7 number of other factors are important. The use of multiple currencies, and associated
8 stoichiometry, is an ongoing topic for model development. Most biological models
9 used in GCMs include a single macronutrient, usually N or P. The exception being the
10 ERSEM family of models (Baretta-Bekker et al., 1997; Blackford et al., 2004; Vichi
11 et al., 2007), which have multiple currencies (C, N, P, Si) and variable carbon and
12 nutrient stoichiometry. The case for including both is for modelling either shelf seas
13 or regions where there are anoxic zones, with associated denitrification; but the latter
14 are not generally observed in the open ocean of the North Atlantic. Nevertheless it
15 may be the case that, unlike in the South Atlantic, the North Atlantic subtropical gyre
16 is depleted in phosphate, possibly as a result of nitrogen fixation enhanced by iron
17 deposition in Saharan dust (Wu et al., 2000). Utilisation of dissolved organic
18 phosphate then becomes an important source of nutrients for primary production in
19 this area (Lomas et al., 2010; Mather et al., 2008). Aeolian dust fluxes have increased
20 during the latter half of the 20th century and models predict that this trend may
21 continue in future (Mahowald et al., 2005). The resulting stimulation of primary
22 production may enhance the biological pump in iron-fertilised regions. However,
23 matters are complicated in that, in order to reproduce biogeochemical feedbacks
24 associated with aeolian dust, models should incorporate the contrasting effects of dust
25 on different microbial groups, as well as associated competitive interactions with
26 phytoplankton (Maranon et al., 2010).

27 Plankton is typically represented in models as belonging to one of two discrete
28 trophic categories: autotrophic phytoplankton or heterotrophic zooplankton. However,
29 the mixotrophs that are found in all aquatic environments (Stoecker, 1998), and play
30 an important role in determining ecological and biogeochemical dynamics, are
31 generally disregarded in ecosystem models. Zubkov and Tarran (1998) found that the
32 photosynthetic phytoplankton accounting for more than 80% of the total chlorophyll

1 in regions of the North Atlantic, were also responsible for 40-95% of the total grazing
2 upon bacteria. These results may have profound implications for our understanding of
3 carbon and nutrient cycling in the North Atlantic and provide a major challenge for
4 future model development.

5 An ever present concern of ecosystem studies (not least modelling) is the
6 availability of an appropriate observation base. However, in addition to scientific
7 cruises and moorings, the last two decades have seen the emergence of new
8 techniques, such as ocean colour satellite sensors and ARGO floats (some of them
9 equipped with oxygen sensors), which providing a continuous monitoring of key
10 biogeochemical variables, and thus opens the possibility of assimilative approach to
11 ecosystem modelling (Brasseur et al., 2009; Ciavatta et al., 2011).

12 Finally, we should take note of a comment made by the great marine ecosystem
13 modelling pioneer Gordon Riley 60 years ago, that a "thorough knowledge of the
14 physiology and ecology of particular species and ecological groups" is a prerequisite for
15 effective ecosystem models, (Riley, 1952). Although our understanding of the
16 competitive interactions of PFTs, as mediated by environment, is improving (e.g.
17 Feng et al., 2009), the extent to which we are in a position to formulate
18 parameterisations for reliable prediction based on this knowledge remains an open
19 question.

20 **Lower trophic level modelling in EURO-BASIN**

21 A fundamental challenge, arising from the issues discussed above, is to find the
22 appropriate level of complexity that will enable ecosystem models to have optimal
23 skill in simulating and predicting biogeochemical fluxes, and also providing
24 appropriate and accurate fields for coupling to HTL models. The ideal level of
25 ecosystem complexity to study ocean biogeochemical processes is an ongoing debate,
26 and as a result many contrasting models are used in the North Atlantic. These models
27 differ not only in their structure, but also in their formulation and the parameterisation
28 of key processes, such as phytoplankton growth, trophic transfer and export of organic
29 matter to the deep ocean. Although diversity in approach can be desirable, a
30 coordinated strategy for comparing models of different complexity should help
31 improve the models, help identify key uncertainties, and ensure compatibility with
32 parallel efforts (e.g. in shelf seas modelling).

1 To try and untangle these problems, a traceable hierarchy of models is a useful
2 concept to consider and this is the approach we adopt in EURO-BASIN. We use
3 NEMO as the general circulation model, with common forcing to harmonise the
4 physical environment for the various ecosystem models and so facilitate the analysis
5 and inter-comparison. Following this approach we will make an ensemble of
6 simulations using a range of simple and more complex ecosystem models. This will
7 allow us to build up a multi-model, multi-scenario 'super-ensemble'. To describe the
8 planktonic ecosystem we have chosen to compare intermediate complexity (PISCES,
9 MEDUSA) with a more complex plankton functional type (ERSEM) model (Figure 8).

10 **PISCES** (Pelagic Interaction Scheme for Carbon and Ecosystem Studies; Aumont et
11 al 2003) considers two phytoplankton (with 4 co-limiting nutrients : N/P/Si/Fe) and
12 two zooplankton, with an explicit semi labile DOM and two particle sizes. Using N as
13 the main currency, as well as P, Si and Fe, it also simulates the C (DIC and alkalinity)
14 and O cycles. The meso pelagic model takes into account particle dynamics between
15 the two sizes, and exchanges between particles, DOM and inorganic pools.

16 **MEDUSA** (Model of Ecosystem Dynamics, nutrient Utilisation and Sequestration;
17 Yool et al 2011) is a modestly complex ecosystem model, it includes two
18 phytoplankton, two zooplankton and three nutrients, and is specifically designed for
19 open ocean applications.

20 **ERSEM** (European Regional Seas Ecosystem Model; Baretta et al 1995) was
21 developed as a generic lower-trophic level/biogeochemical cycling model. ERSEM is
22 an intermediate/high complexity model originally designed for simulating shelf seas
23 biogeochemistry and ecosystem function. ERSEM simultaneously describes pelagic
24 and benthic ecosystems in terms of phytoplankton, bacteria, zooplankton, zoobenthos,
25 and the biogeochemical cycling of C, N, P, Si.

26 By running these different models in the same physical environment we can begin
27 to quantify structural and parameter uncertainty. This diversity of models is required
28 for two reasons. First they extend the range of scenarios and therefore give a
29 constraint on the combined parameter and structural uncertainty. Second, and perhaps
30 more importantly as we are still learning how to model these processes, they inform
31 future model development through the comparison of approaches with an in-depth

1 analysis of the biogeochemical fluxes involved and through validation against
2 available *in-situ* and remote sensing data.

3 Here, we illustrate the approach using existing model simulations and compare
4 results from three global applications of these three LTL models. Each exists within a
5 similar, but not identical physical framework (e.g. some differences in resolution and
6 atmospheric forcing; Table 2), so we limit our discussion here to a qualitative
7 assessment. Figure 9 shows a meridional (N-S) surface chlorophyll transect of the
8 North Atlantic for all three models and SeaWifs ocean colour based chlorophyll. In all
9 cases, between 25°N and 50°N the models reproduce the spatial trends and
10 concentrations of chlorophyll quite well, but underestimate the chlorophyll
11 concentrations south of 25°N. The largest differences between the models occur north
12 of 50°N; an explanation for this has yet to be established. Figure 10 shows a
13 comparison of annual mean surface chlorophyll and phytoplankton community
14 structure for the three models in terms of diatoms and non-diatoms for the period
15 1998-2004 for the three models. In addition we also show the equivalent satellite
16 phytoplankton community structure data product derived from SeaWifs (Brewin et al.,
17 2010b; Hirata et al., 2011).

18 All the models produce the general observed north-south trend in chlorophyll
19 concentration and diatom distribution, with both chlorophyll and diatoms dominating
20 in the north of the domain (Figure 9, 10). This suggests to a first order the emergent
21 property of this simple community structure functions well in all three models.
22 However, the modelled diatom fraction appears overestimated in all three models
23 compared with the satellite product. The question remains whether or not these
24 discrepancies are a function of the physical model, the biogeochemical models or
25 some combination of both, alongside observational uncertainty.

26 The impact of the coarse scale physics is apparent in all the simulations, an aspect
27 that will be specifically addressed in EURO-BASIN. The satellite chlorophyll clearly
28 shows that the high chlorophyll concentrations in the North Atlantic lie to the north of
29 the Gulf Stream. In the models the high chlorophyll extends further south, showing a
30 much more diffuse boundary with the sub-tropical gyre, which in turn is too far south
31 in all the models. This is most likely due to the poor representation of mesoscale
32 physics on the northern boundary of the gyre and highlights a major challenge: that of

1 disentangling the performance of the biogeochemical model from that of the physics.
2 It may be in many cases that the performance of the biogeochemical models is
3 masked by that of the physics. There is a need for metrics that assess the fidelity of
4 the biogeochemical processes independently of the physics, which points to the role
5 of meta-analysis to define robust testable global relationships between
6 biogeochemical variables.

7 To illustrate this point we draw on a meta-analysis of over 3000 observations of
8 collocated HPLC chlorophyll and accessory pigment data, which shows that there is a
9 robust empirical relationship between chlorophyll concentration and the fraction of
10 diatoms in the community (Hirata et al., 2011). Diatoms dominate at chlorophyll
11 concentrations above 1 mg chl m^{-3} . Figure 11 shows density plots illustrating the
12 relationship between chlorophyll and the % diatom fraction for all three models, and
13 SeaWifs as a reference. In all cases the models capture the observed response of
14 increasing diatom fraction with increasing chlorophyll concentration; however
15 MEDUSA and PISCES systematically over-estimate the diatom fraction. The crucial
16 point is not the performance of the respective models per se, but the fact that we can
17 see a general response of the plankton models (in this case an emergent relation
18 between community and chlorophyll) that is independent of the hydrodynamic model.

19 **4. Higher Trophic Levels modelling: state of the art,** 20 **challenges and gaps**

21 Alongside models focusing on biogeochemistry and LTLs, such as those
22 considered above, are models that aim to capture other aspects of the ecosystem in
23 some detail. Examples include models that represent foodwebs, species behaviour and
24 interaction, and the structure and function of the whole ecosystem. As with physical
25 models, the different characteristics and questions relevant to open ocean and coastal
26 ecosystems have led to a diversity of modelling approaches that is still growing
27 rapidly. Moreover, due to the societal and economical value of many exploited living
28 marine resources, a substantial effort has been devoted over the last decades to the
29 development of specific population models for the management of fisheries. In the
30 open ocean, the focus is on large pelagic and highly migrant species, like tunas and
31 billfishes, which feed opportunistically on a large range of micronektonic forage

1 species (size ~ 1-20 cm). In shelf seas, exploited species include bottom (e.g., plaice,
2 halibut), demersal (e.g., cod, hake) and small to medium size pelagic species (e.g.,
3 herring, mackerel blue whiting, sardines, anchovies). These feed on benthic organisms
4 as well as zooplankton.

5 Past food web studies have tended to treat the upper and lower trophic levels
6 separately; the use of detailed simulations of physical dynamics requires some
7 limitation on biology. This led de Young et al (2004) to propose that “rather than
8 model the entire ecosystem we should focus on key target species and develop
9 species-centric models”. The focus of benthos and the upper trophic level studies is
10 often on predatory interactions based on fish diet data (Garrison and Link, 2000;
11 Heath, 2005). Linear, steady-state, food-web models have been used to represent
12 these complex interactions (Pauly and Christensen, 1993). This trophic-centric
13 approach does not include the dynamics of individual species and neglects the
14 physical processes. Steele and Gifford (2010) argue that these two sets of simplifying
15 assumptions are complementary and answer different questions about the dynamics of
16 individual populations and the productivity of ecosystems.

17 Recently, in response to the desire to move towards an ecosystem-based approach
18 to marine management, end-to-end models representing the entire trophic structure
19 and physical components of the ecosystem at a fine spatial scale have been developed
20 (Cury et al., 2008; Rose et al., 2010). One approach is to combine aggregated versions
21 of existing food web models of the upper trophic levels, with NPZD formulations of
22 the microbial web, and with simplified representations of the main physical forcing
23 (e.g. Kearney et al., 2012; Steele et al., 2007; Steele and Ruzicka, 2011). The critical
24 issue is whether the use of functionally defined groups or guilds, rather than species,
25 as variables, can achieve portability, while retaining adequate realism.

26 The small pelagic species group in particular is strongly dependent on the
27 abundance of a few copepod species (*Calanus spp.*) that dominate the
28 mesozooplankton in the North Atlantic Basin. This motivates the development of
29 specific models to study the complex life histories of these zooplankton species.

30

31

1 **Copepods**

2 Copepods have several developmental stages from eggs through nauplii and
3 copepodites to adults, as well as a diapauses stage, in deep water over winter. Marked
4 differences exist between species. For example, copepods that inhabit the North
5 Pacific are relatively large and have a single generation per year, as compared to the
6 smaller copepods in the North Atlantic, which undergo several generations per year
7 (Parsons and Lalli, 1988). A complicating factor in the North Atlantic is that there are
8 two dominant species: *Calanus finmarchicus* and *Calanus helgolandicus*, with
9 distinct niches. The former is adapted to the colder temperatures of the northwest
10 North Atlantic, in contrast to *Calanus helgolandicus* which prefers warmer
11 temperatures and dominate further south and east (Helaouet and Beaugrand, 2007).
12 Changes in temperature, for example due to climate change and variability, could
13 therefore significantly impact on the distribution of these two species (Moller et al.,
14 2012), with potential impacts on the recruitment of Atlantic cod (Beaugrand et al.,
15 2003a).

16 A number of copepod population models have been developed that target the
17 distributions and production of key species. For example, Carlotti and Radach (1996)
18 studied the seasonal dynamics of *Calanus finmarchicus* in the North Sea using a one-
19 dimensional water column model. Heath et al (1997) used a Lagrangian 1D approach,
20 using output from a 3-D hydrodynamic model, to study the dynamics of *Calanus* in
21 the Fair Isle channel (northern North Sea). Three-dimensional approaches have also
22 been adopted, for example, Bryant et al.'s (1997) study of the seasonal dynamics of
23 *Calanus finmarchicus* in the northern North Sea and Stegert et al.'s (2009) study of
24 the population dynamics of *Pseudocalanus elongatus* in the German Bight (North
25 Sea). Regarding the North Atlantic, a major modelling study was undertaken by
26 Spiers et al. (2006; 2005), examining the distribution and demography of *Calanus*
27 *finmarchicus*. The model followed progression from eggs through six naupliar stages,
28 five copepodite stages and adults. An interesting aspect of the study is that it explored
29 the mechanisms controlling diapause, suggesting that irradiance may be an important
30 cue for both the onset of, and awakening from, diapause (Spiers et al., 2005).
31 However, the application of population-based models, which represent life history in
32 terms of age and developmental stage of body weight, within biogeochemical models

1 is problematic (Carlotti and Poggiale, 2010). There are substantial technical
2 challenges and computational requirements associated with highly resolved
3 population models in 3-D. At a more fundamental level, a significant challenge in
4 modelling species such as *Calanus finmarchicus* is that many aspects of its biology
5 are poorly understood (Spiers et al., 2006). The mechanisms involved with diapause
6 provide one good example.

7 Individual Based Models (IBMs) keep track of each individual in a population, in a
8 primarily Lagrangian framework (DeAngelis et al., 1979; DeAngelis and Gross, 1992;
9 Grimm and Railsback, 2005). In these models individuals can be characterised by
10 state variables such as weight, age and length, and they may also allow behavioural
11 strategies to be implemented in a spatial context. This allows the properties of a
12 population to be described by the properties of its constituent individuals. Model
13 validations against data can be done at the individual level; matching the
14 observational approach. Moreover, models based on individuals benefit from having
15 the same basic unit as natural selection. This makes IBMs appealing for addressing
16 behavioural and life history tradeoffs and therefore for studying higher trophic levels,
17 which can have a great behavioural repertoire, in particular in relation to motility.
18 Consequently individual based modelling is used extensively for modelling higher
19 trophic levels in EURO-BASIN. There have been several applications of IBMs to
20 zooplankton in the North Atlantic. Early studies focused on simulating drift
21 trajectories of individual plankton and their growth, survival and reproduction
22 (Carlotti and Wolf, 1998; Miller et al., 1998). Models have subsequently been fitted
23 with adaptive traits in order to investigate the consequences for adaptation and
24 population dynamics of different levels of environmental forcing (Fiksen, 2000; Huse,
25 2005). More recently there have been applications using super-individuals that allow
26 entire populations of zooplankton to be simulated with an individual based
27 representation (Hjøllo et al., 2012).

28 **Open ocean Mid-Trophic Levels (MTL)**

29 For a basin or global scale modelling, an exhaustive representation of all mid-
30 trophic level species is unrealistic and unnecessary. It is more appropriate to consider
31 a hybrid approach combining functional groups of forage species (e.g., mesopelagic
32 fish) and specific detailed population submodels for a few species of interest (herring

1 sardines, etc). On the top of this the approach should also consider the large oceanic
2 predator species, fisheries and associated fishing mortality. Ideally, in such an
3 integrated approach, each functional group would include specific population model
4 representations, either based on Lagrangian (IBM) or Eulerian approaches. While this
5 vision may appear ambitious and technically challenging, the level of computation
6 can be drastically reduced for these specific population submodels, using a 2D or
7 layer-based 3D approach, and degrading the spatial resolution of the physical model.
8 Key components of this integrated approach for MTL modelling already exist or are
9 the subject of ongoing developments. Moreover, there are examples of modelling
10 approaches of MTL functional groups that have been developed to link lower
11 biogeochemical models to population dynamics of large oceanic predators that can be
12 drawn upon.

13 One such approach proposes a representation of basin-scale spatiotemporal
14 dynamics of six functional groups of MTLs (Lehodey et al., 2010), here applied to the
15 North Atlantic. The definition of these groups is based on the occurrence or absence
16 of diel migration between the surface (epipelagic), subsurface (mesopelagic) and deep
17 (bathypelagic) layers (Figure 12). Their dynamics are driven by temperature, currents,
18 primary production and euphotic depth simulated by a coupled physical-
19 biogeochemical model. The vertical structure is currently a simplified 3-layer ocean,
20 and to obtain the biomass during the day and night in each layer, the components are
21 summed according to their day and night position (Figure 12). Recruitment, ageing,
22 mortality and passive transport by horizontal currents are modelled within an Eulerian
23 framework, taking into account the vertical migration of organisms. The temporal
24 dynamics are based on a relationship linking temperature and the time of development
25 of MTL organisms, using macroecological principles that define the energy transfer
26 through the biomass size spectrum (Brown et al., 2004; Dickie, 1976; Jennings et al.,
27 2002; Kerr, 1974). Since the dynamics are represented by this well established
28 relationship, there are only six parameters in the model that need to be estimated. The
29 first defines the total energy transfer between primary production and all the MTL
30 groups, while the others are relative coefficients, redistributing this energy through
31 the different components. A notable advantage of this simplified approach is that it
32 facilitates the optimization of parameters through the assimilation of acoustic data. In

1 particular, the matrix of size distribution coefficients can be straightforwardly
2 estimated using relative day and night values of acoustic backscatter, integrated in
3 each of the three vertical layers of the model. This facilitates the use of different un-
4 standardized acoustic profiles (Handegard et al., In Press) in constraining the model.

5 **Small pelagic fish**

6 Models simulating the drift of fish eggs and larvae using Lagrangian approaches
7 have become commonplace in the last few decades, but there are still rather few
8 comparable models for adult fish. The added complexity of addressing the greater
9 behavioural repertoire of adult fish adds challenges to the modelling. With regards to
10 the North Atlantic, models have been developed for the Barents Sea capelin (*Mallotus*
11 *villosus*), where the focus has been on simulating the movement from first principles
12 (Huse, 2001); relatively few IBMs focus on simulating the entire life cycle of fish
13 stocks. Initial attempts were made in this to study the Barents Sea capelin (Huse,
14 1998; Huse and Ellingsen, 2008), which illustrated the flexibility of the individual
15 based approach in coupling movement, behaviour with growth, survival and
16 eventually recruitment under different climate scenarios (Huse and Ellingsen, 2008).

17 **Large oceanic species**

18 The distribution of micronekton is a prerequisite for modelling the spatial
19 dynamics of their predators, i.e., the large pelagic species such as tuna and swordfish.
20 The Spatial Ecosystem and Population Dynamics Model (SEAPODYM) uses this
21 distribution to simulate the full life cycle of the large pelagic species from eggs to
22 oldest adults (Lehodey et al., 2008). The SEAPODYM model includes: a definition of
23 spawning, local movements as the responses to habitat quality and also through basin-
24 scale seasonal migrations, accessibility of forage for fish within different vertical
25 layers, predation and senescence mortality and its change due to environmental
26 conditions. Data assimilation techniques, based on an adjoint method and a maximum
27 likelihood approach, are implemented to assist the parameterization using historical
28 fishing data (Senina et al., 2008).

29 In the North Atlantic basin, albacore tuna (*Thunnus alalunga*) has been one of the
30 most exploited pelagic species (Arrizabalaga et al., 2004), and shows a major and
31 steady declining trend during the last 40 years. It is unclear if this decline is due to

1 overfishing, shift of fisheries to other target species or changes in environmental
2 conditions (e.g. climate change and variability). The preliminary application of
3 SEAPODYM model to this species suggests that the environment has been a strong
4 driver in the observed trend of the last decades (Figure 13). In particular, the model
5 predicts changes in biomass of micronekton in the tropical region that are linked to
6 changes in temperature predicted by the ocean GCM (NEMO-ORCA2 forced by
7 NCEP reanalysis); this still needs to be validated with observations.

8 **Trophic cascades and two way coupling**

9 The example of Atlantic albacore tuna suggests a combined effect of fishing and
10 bottom-up forcing; these are usually thought to be the main forcing in the open-ocean
11 systems (Steele, 1998). Top-down effects, or trophic cascades (Pace et al., 1999),
12 have as yet only been detected in the ecosystems of some shelf and enclosed seas, for
13 example, the Black Sea (Daskalov et al., 2007), the Baltic Sea (Casini et al., 2008;
14 Mollmann et al., 2008) and parts of the shelf seas of the Northwest Atlantic (Frank et
15 al., 2005; Frank et al., 2006; Myers et al., 2007). But there are now strong indications
16 of top down control from planktivorous fish on zooplankton in the Norwegian Sea
17 (Huse et al., 2012). This suggests that top down control can be important for basin
18 scale ocean areas as well. Trophic cascades occur when the abundance of a top
19 predator is decreased, releasing the trophic level below from predation. The released
20 trophic level reacts by an increase in abundance, which imposes an increased
21 predation pressure on the next lower trophic level, and so on. The occurrence of
22 trophic cascades is dependent on temperature (high temperature leads to faster growth
23 rates and therefore less sensitivity to fishing) and diversity (higher diversity stabilizes
24 the system; Ciannelli et al., 2005; Frank et al., 2007). Frank et al. (2007) stated that
25 cold and species-poor areas such as the North Atlantic might readily succumb to
26 structuring by top-down control and recover slowly (if ever). In contrast, warmer
27 areas with more species might oscillate between top-down and bottom-up control,
28 depending on exploitation rates and, possibly, changing temperature regimes.
29 Nevertheless, the heavily exploited North Sea seems do not to show any sign of
30 trophic cascade (Reid et al., 2000).

31 Different approaches are necessary to investigate and model the two-way coupling
32 between lower and upper trophic levels within their physical and chemical

1 environment. As noted above, the shelf seas of the northern Atlantic Basin are
2 dominated by small pelagic species (e.g., herring, sardines, anchovy, capelin), for
3 which the coupling should occur at the zooplankton level that provides the bulk of
4 prey biomass to small pelagics. Then, sensitivity analyses simulating changes in
5 fishing mortality of these commercial species can help explore the top down effect of
6 these changes. However, there is often a group of a few species that share the same
7 ecosystem, with their abundance fluctuating according to their own dynamics and in
8 response to environmental variability and top-down factors (fishing or predation).
9 Thus, multi-species models of small pelagic populations appear to be necessary to
10 achieve a minimum degree of realism.

11 For the basin scale pelagic system, where exploited species are at a higher trophic
12 level (tuna, swordfish), a first necessary step would be to shift the closure term in the
13 LTL model to the next trophic level, i.e. to MTLs. These new functional groups can
14 be coupled to zooplankton and POC model variables directly through predation and
15 mortality rates. However, since this parameterization is very challenging, an
16 alternative would be to use the spatio-temporal dynamics of MTL groups, as already
17 simulated above, to introduce relative variability around the average parameters of
18 zooplankton mortality and POC production that are already estimated in current
19 biogeochemical models. For example, a high (low) biomass of MTL would be
20 translated through an increase (decrease) of the average mortality coefficient of
21 zooplankton, in a given range that guarantees the numerical stability of the simulation.
22 From this extension of ocean ecosystem models to MTL functional groups, a first
23 expected result would be a better representation of zooplankton grazing, integrating
24 spatial and temporal shifts in grazing pressure due to the dynamics of MTL organisms
25 themselves. In addition, a better dynamical representation of processes in detritus
26 uptake and release by meso- and bathy pelagic organisms might be expected.

27 Beyond this, spatial population dynamics models of large marine predator species
28 and their fisheries would need to be coupled to MTL components through their
29 predation on these groups. Here also the parameterization of predation rates is
30 challenging, especially if not all the predators species are included in the model.
31 However, as with the coupling between MTL and LTL, a similar alternative could be
32 to work, at least in a first instance, in terms of relative variability that does not prevent

1 the exploration of the propagation of the top-down signal due to fishing pressure to
2 the lowest trophic level.

3 **Higher trophic level modelling in BASIN**

4 Modelling the top-down effects of fishing on oceanic mid-trophic and lower trophic
5 levels requires not only the two-way coupling of these different components of the
6 ecosystem, but first and foremost the correct quantitative estimate of biomass and
7 spatial dynamics of higher trophic levels under the influence of both environmental
8 variability and fishing impacts. Unfortunately, despite a large effort to develop
9 quantitative approaches for stock assessment over the past 50 years, a large
10 uncertainty remains on many exploited stocks concerning their total biomass and their
11 spatio-temporal dynamics. There is still a long way to go to reconcile the recent
12 progress achieved in physical and biogeochemical/LTL oceanography on the one
13 hand and marine ecology, focusing on spatial dynamics and population dynamics on
14 quantitative estimate of change of abundance in time, on the other hand. The Euro-
15 Basin project is a strong pluridisciplinary effort toward this goal. Below we
16 summaries the key higher trophic level models applied in the EURO-BASIN project.

17 **NORWECOM (IBM)** The Norwegian Ecological model system NORWECOM
18 (Aksnes et al., 1995; Skogen et al., 2007) was originally a biogeochemical model
19 system with two functional groups: diatoms and flagellates. This model has recently
20 been coupled to an IBM for the copepod *Calanus finmarchicus* (Hjøllo et al., 2012)
21 and the planktivorous fish stock Norwegian spring spawning herring, blue whiting
22 and mackerel (Utne et al., 2012). These developments are part of an ongoing plan to
23 develop this into NORWECOM.E2E, or a full end-to-end model system. This model
24 system has recently been applied to simulate the interactions between fish stocks in
25 the Norwegian Sea and their utilisation of common zooplankton resources (Huse et al.,
26 2012). Within EURO-BASIN, NORWECOM will be used to address the trophic
27 couplings in the Norwegian Sea and the *Calanus* component will be integrated with
28 NEMO and ERSEM to study *Calanus* dynamics within its entire distributional range.

29 **APECOSM** The Apex Predators ECOSystem Model (Maury et al., 2007a; Maury et
30 al., 2007b) is a spatially explicit size based model of open ocean ecosystems, based on
31 a Dynamic Energy Budget approach. It is two-way coupled to the PISCES ecosystem

1 model which in turn is coupled to the 1/4° NEMO North Atlantic physical model.
2 APECOSM's philosophy is to specify a very generic and robust structure of marine
3 ecosystems from which particular regional ecosystem organization emerges due to
4 interactions with the environment. It relies on a very few general rules from which the
5 structure of the model and the parameterizations are derived mechanistically.
6 APECOSM represents the flow of energy through the ecosystem with a size-resolved
7 structure horizontally and with time. The uptake and use of energy for growth,
8 maintenance and reproduction by the organisms are modelled according to the DEB
9 (dynamic energy budget) theory (Kooijmann, 2000) and the size-structured nature of
10 predation is explicit. Distinction between the epipelagic community, the mesopelagic
11 community and the migratory community that experiences nyctemeral vertical
12 movements and hence transfers energy between the two other communities is also
13 expressed; their habitat depends mainly on the light profile. Thus, size and
14 spatiotemporal co-occurrence of organisms structure trophic interactions.

15 **SEAPODYM-MTL (MTL) Spatial Ecosystem and Population Dynamics Model-**
16 **Mid Trophic Levels** (Lehodey et al., 2010). As already described above in more
17 detail, this is a three-layer bulk biomass functional type pelagic- ecosystem model
18 combining energetic and functional approaches based on the vertical behaviour of
19 organisms and following a temperature-linked time development relationship.

20 How these models are brought together with the physical and LTL models is
21 summarised in section 6.

22 **5. Climate change projections for marine ecosystems** 23 **of the North Atlantic**

24 In order to define the envelope of response to climate change of marine ecosystem
25 function, we must establish a range of scenarios that encompass possible future
26 conditions that are scientifically and societally plausible. Coupled atmosphere-ocean
27 general circulation models (AO-GCMs) provide the best available source of
28 information for this purpose on a global scale, but this information is generally on too
29 coarse a grid scale to be relevant for many regional scale studies, and so limits the
30 application of the models. Moreover, even on a basin scale, mesoscale activity makes
31 up a crucial component of the dynamics of the North Atlantic, and hence potential

1 changes to its physics; this activity is absent in the majority of the ocean components
2 of the current generation of AO-GCMs. Similarly shelf sea processes (e.g. tides and
3 coastal currents) are not generally represented. Hence, a downscaling procedure is
4 required: the AO-GCM is used to provide boundary conditions (surface and in some
5 cases lateral) for EURO-BASIN models of finer resolution and more appropriate
6 process representation.

7 Alongside the choice of AO-GCM forcing are two important considerations: the
8 emissions scenario(s) and the forecast horizon. The emissions scenarios prescribe the
9 atmospheric concentrations of radiatively active constituents, which in turn determine
10 the radiative forcing of the AO-GCM. These are either derived from a socio-economic
11 ‘story-line’ or prescribed to specific values (RCP’s). The forecast horizon dictates
12 how far into the future the model simulations will be conducted. The crucial issue
13 here in climate change studies is whether a significant signal can be detected against
14 the background of natural variability. This is a crucial factor for the North Atlantic,
15 where this variability is exceptionally large.

16 The uncertainty in future projections can then be thought of as being a combination
17 a three factors: scenario uncertainty (reflecting the unknown future socio-economic
18 landscape), model uncertainty (reflecting inaccuracies in the model; this can be
19 characterised to some extent by comparing different modelling approaches) and
20 internal variability (reflecting the difficulty in detecting a clear climate change signal
21 until this ‘averages out’). This is well illustrated, in the global context, by the work of
22 Hawkins and Sutton (2009), which shows how model and “internal variability”
23 uncertainty decrease with lead time, but scenario uncertainty increases, and that by
24 moving from a global to a regional scale the model and internal variability uncertainty
25 can substantially increase. They also show that the European region has particularly
26 strong internal variability (in this case in air temperature).

27 When we move to the climate impacts arena we add other aspects of uncertainty
28 arising from, and propagating through, the downscaled models. Practicalities limit our
29 ability to at best span aspects of the uncertainty with a limited number of simulations.
30 Such an approach is an important first step and allows us to explore the system’s
31 response to the range of different drivers both qualitatively and quantitatively.

1 However, the usefulness of the results as ‘forecasts of future conditions’ is
2 questionable, as discussed by Skogen et al (2011).

3 The opening question for explorations of climate change impacts tends to be ‘how
4 might anthropogenic climate change impact this process in the future?’ An issue that
5 immediately arises is that the forecast horizon required for the answer to be relevant,
6 to policy decisions being considered now, is generally much shorter than that required
7 to give a clear answer; i.e. the policy relevant time scales more closely match those of
8 the natural variability than the longer term trends. For example, the planning cycle for
9 MSFD is 6-years, so only a projection of many such cycles ahead will give a clear
10 climate change signal against the background of natural variability. This is especially
11 the case in regions, such as the North Atlantic, where natural variability arising from
12 (e.g.) the position of the storm track and atmospheric processes such as blocking are
13 so important. Moreover processes that are themselves non-linearly dependent on this
14 natural variability, such as aspects of ecosystem function, are likely to exacerbate this
15 issue through an exaggerated sensitivity to the details of the variability (e.g. through
16 mixed layer depths). This mismatch between the time scales on which we can make
17 clear statements on climate change, and the time scales over which decisions need to
18 be made is a grand challenge in climate change impacts work. A possible mitigating
19 effect is that ecosystems can act as integrators of their environmental conditions and
20 so improve signal-to-noise ratios over their forcing, allowing for the detection of
21 weaker climate change signals (Taylor et al., 2002). Hence it is more appropriate to
22 re-frame the question so that climate change and variability are on a more equal
23 footing, and ask: ‘what is the range of possible impacts on this process, given present
24 day statistics of variability and how they might change into the future?’.

25 An appropriate forecast horizon for EURO-BASIN is out to 2040, since this is
26 most relevant for the issues of ecosystem function and their relation to (e.g.) fisheries
27 and climate change mitigation policy. On this basis it is appropriate to use transient
28 simulations here, which run continuously from the present to the future, rather than
29 the ‘time-slice’ approach that is common in many downscaling type simulations (e.g.
30 (Holt et al., 2012a).

31 The forcing we consider must, therefore, treat the atmospheric dynamics and
32 consequent natural variability as accurately as possible, and the analysis needs to

1 explicitly capture the modes of response of the system. For example, inadequacies in
2 the representation of the North Atlantic storm tracks (being too far south) in the AR4
3 class have previously been identified (Lowe et al., 2009), and whether this is rectified
4 in the CMIP5 models needs to be critically examined. Such biases can have serious
5 consequences when exploring the impact of climate change on the higher trophic
6 levels of the ecosystem (Lehodey et al., 2012; Stock et al., 2011). A particular
7 consideration for this study, is that the phase of the variability in AOGCM forced
8 simulations is not constrained by observations, so the longer period modes (e.g. the
9 Atlantic Multi Decadal Oscillation (AMDO); and Atlantic Meridional Mode; see
10 Grossmann and Klotzbach, 2009) almost certainly will not be in the appropriate phase
11 for a 2040 projection and the forecast horizon is not sufficient for these to average out
12 in the statistics. The decadal climate prediction models used in CMIP5 (Taylor et al.,
13 2012), whereby the climate model is initialised from present day observations, have
14 the potential to address this. Recent investigations of the ensemble of these models
15 suggests that they have some skill in retaining the AMDO, with correlations at around
16 the 90% significant level out to 9 years lead time (Kim et al., 2012), but beyond this
17 scenario forcing becomes increasingly important (Branstator and Teng, 2012).

18 For EURO-BASIN, we adopt two approaches. First, the conventional approach and
19 conduct a series of simulations forced by a small number of free-running CMIP5
20 AOGCM simulations, accepting that the phase of variability will not be coincident
21 with reality; the simulations will be long enough to average out some of this (e.g. the
22 North Atlantic Oscillation). The second approach also uses the CMIP5 outputs, but
23 aims to correct the biases by perturbing a reanalysis based hindcast forcing set (DFS5;
24 an update on Brodeau et al 2010). The DFS5 atmospheric data is decomposed into
25 realistic weather regimes, and analogs of these are defined in the AOGCM
26 simulations of the present-day period. The evolution of these analogs is then
27 statistically followed in future scenario IPCC simulations, and a forcing data for
28 future simulations is constructed with these time evolutions, using the realistic
29 weather regime previously defined (Cassou et al., 2011; Minvielle et al., 2011). Hence,
30 the realism of the spatial structure of the future forcing is maintained and the
31 evolution of the future forcing is given by statistics from the IPCC runs. Moreover,

1 there is continuity and consistency between the (realistic) hindcast and forecast
2 forcing.

3 **6. Concluding remarks: Integrating the Euro-Basin**

4 **Models**

5 EURO-BASIN is focused on creating predictive **understanding of key species and**
6 **the emergent ecosystem and biogeochemical features of the North Atlantic basin**
7 **in order to further the abilities to understand, predict and contribute to the**
8 **development and implementations of the ecosystem approach to resource**
9 **management.**

10 In order to link ecosystems and key species to carbon fluxes EURO-BASIN follows a
11 trophic cascade framework, quantifying the flow of mass and elements between key
12 species and groups, along with a size spectrum approach to establish and quantify the
13 links between these trophic levels and assess the implications of changes in the
14 players on the flux of carbon. To deliver this we draw on the state of the art in
15 numerical modelling of the North Atlantic: high resolution ocean physics,
16 biogeochemical models of differing complexity, and a range of approaches to
17 modelling mid and higher trophic levels are employed. Figure 14 illustrates how the
18 various modelling tools for assessing ecosystem characteristics discussed in this paper
19 relate to each other and the stressors influencing the trophic cascade from primary
20 producers to top predators. How this will proceed in practice in Euro-Basin can be
21 summarised as follows:

22 **1. Physics Biogeochemistry Coupler:** The three biogeochemical models (ERSEM,
23 MEDUSA, PISCES) have been coupled with NEMO. There are three configuration of
24 NEMO in use in Euro Basin;

- 25 i) 1/4° N Atlantic Basin: ERSEM, PISCES
- 26 ii) 1/4° Global Ocean: Medusa
- 27 iii) 1/12° NN Atlantic model (with shelf seas processes): ERSEM

28 The 1/4° domains are used for the regional hindcast, climate forced and re-analysis
29 forced simulations, climate-scenario forced simulations, top down control
30 perturbation experiments and a fully coupled end to end ecosystem model. The 1/12

1 model is for use in assessing the sensitivity of ecosystem response to key processes
2 relating to mesoscale physics, shelf seas physics and spatial scale.

3 **2. MTL model coupling 1 way:** The suite of MTL models (MTL; APECOSM and the
4 IBM) will be coupled off-line to the ensemble averages of the planktonic ecosystem
5 states from the LTL reanalysis and future climate simulations (point 1).

6 **3. ERSEM- IBM coupler:** 2 way coupling of ERSEM with the Calanus IBM.

7 **4. PISCES –APECOSM coupler:** 2 way coupling of PISCES with the APECOSM.

8 **5. Parameterisation Convection IBM:** The Convection IBM model is being
9 developed to explore the impact of deep convection on phytoplankton growth. The
10 goal is to inform the parameterisation of these processes in the Eulerian frameworks
11 of the biogeochemical models.

12 **6. Parameterisations of C export:** An analysis of existing algorithms for particle flux
13 and based on historic observations and fieldwork is being undertaken (Sanders et al
14 this volume). Based on the recommendations from this work, parameterisations of
15 particle flux will be amended and tested in the LTL models as appropriate.

16 **7. Habitats and estimates of top down control:** To assess the sensitivity of
17 biogeochemical cycles to changes in grazing pressure, we will draw on information
18 on habitats predation rates from other components in Euro-Basin to design sensitivity
19 experiments. Specifically, the development of habitat models will provide information
20 for the validation of modelled biogeography, and estimates of herring, blue whiting
21 and mackerel predation on LTL to help parameterise sensitivity experiment to top
22 down control on biogeochemical cycles.

23 **8. Model outputs to drive economic and management models:** The integrative
24 modelling will provide model outputs for facilitate other activities in Euro-basin,
25 specifically

- 26 i) MTL biomass estimates to drive tuna models
- 27 ii) LTL biomass estimates to drive herring, blue whiting and mackerel models
- 28 iii) Primary production to drive bioclimatic envelope models of fish.

- 1 iv) Carbon budgets to estimating the economic value of the N Atlantic C pump.
 2 v) Hydrodynamic and biogeochemical information to drive the models
 3 underpinning the comparative analysis of foodweb structure.
 4 vi) LTL biomass estimates for the integrative analysis of past and future
 5 ecosystem change, using Artificial neural networks.
 6 vii) Habitat information for advancing fisheries management.

7 Hence, these tools will be used both singly and in combination to assess the emergent
 8 properties of the ecosystems, to create metrics for the prediction of future states and to
 9 contribute to the assessment and implementation of an ecosystem approach for the
 10 management of exploited resources. Full details of the on-going Basin-scale
 11 Integrative Modelling work in EURO-BASIN and the results as they emerge can be
 12 found at <http://www.EURO-BASIN.eu/>.

13 **Acknowledgements:**

14 This review was funded by EC 7th Framework Programme through the EURO-
 15 BASIN Integrated Project on Basin-Scale Analysis, Synthesis and INtegration
 16 (Contract 264933). Altimetry data used in this study were developed, validated, and
 17 distributed by the CTOH/LEGOS, France.

18 **References**

- 19 Adcroft, A., 2013. Representation of topography by porous barriers and objective
 20 interpolation of topographic data. *Ocean Modelling*, 67, 13-27.
 21 Adcroft, A., Hill, C., Marshall, J., 1997. Representation of topography by shaved cells
 22 in a height coordinate ocean model. *Monthly Weather Review*, 125, 2293-2315.
 23 Aksnes, D.L., Ulvestad, K.B., Baliño, B.M., Berntsen, J., Egge, J.K., Svendsen, E.,
 24 1995. Ecological modelling in coastal waters: Towards predictive physical-chemical-
 25 biological simulation models. *Ophelia*, 41, 5-36.
 26 Allen, J., Brown, L., Sanders, R., Moore, C., Mustard, A., Fielding, S., Lucas, M.,
 27 Rixen, M., Savidge, G., Henson, S., 2005. Diatom carbon export enhanced by silicate
 28 upwelling in the northeast atlantic. *Nature*, 437, 728-732.
 29 Allen, J.I., Blackford, J., Holt, J.T., Proctor, R., Ashworth, M., Siddorn, J., 2001. A
 30 highly spatially resolved ecosystem model for the North West European continental
 31 shelf. *SARSIA*, 86, 423-440.
 32 Allen, J.I., Siddorn, J.R., Blackford, J.C., Gilbert, F.J., 2004. Turbulence as a control
 33 on the microbial loop in a temperate seasonally stratified marine systems model.
 34 *Journal of Sea Research*, 52, 1-20.

- 1 Anderson, T., Pondaven, P., 2003. Non-Redfield carbon and nitrogen cycling in the
2 Sargasso Sea: pelagic imbalances and export flux. *Deep-Sea Research I*, 50(5), 573–
3 591.
- 4 Anderson, T.R., 2005. Plankton functional type modelling: running before we can
5 walk? *Journal of Plankton Research*, 27, 1073-1081.
- 6 Anderson, T.R., Williams, P.J.L., 1998. Modelling the seasonal cycle of dissolved
7 organic carbon at station E-1 in the English Channel. *Estuarine Coastal and Shelf
8 Science*, 46, 93-109.
- 9 Arrizabalaga, H., Costas, E., Juste, J., Gonzalez-Garces, A., Nieto, B., Lopez-Rodas,
10 V., 2004. Population structure of albacore *Thunnus alalunga* inferred from blood
11 groups and tag-recapture analyses. *Marine Ecology Progress Series*, 282, 245-252.
- 12 Aumont, O., Maier-Reimer, E., Blain, S., Monfray, P., 2003. An ecosystem model of
13 the global ocean including Fe, Si, P colimitations. *Global Biogeochemical Cycles*, 17,
14 26.
- 15 Backhaus, J.O., Hainbucher, D., 1987. A Finite-Difference General Circulation Model
16 for Shelf Seas and its Application to Low Frequency Variability on the North
17 European Shelf. In J.C.J.N.a.B.M. Jamart (Ed.), *Three-Dimensional Models of Marine
18 and Estuarine Dynamics*, Vol. 45 (pp. 221-244).
- 19 Backhaus, J.O., Hegseth, E.N., Wehde, H., Irigoien, X., Hatten, K., Logemann, K.,
20 2003. Convection and primary production in winter. *Marine Ecology Progress Series*,
21 251, 1-14.
- 22 Badin, G., Williams, R.G., Holt, J.T., Fernand, L.J., 2009. Are mesoscale eddies in
23 shelf seas formed by baroclinic instability of tidal fronts? *Journal of Geophysical
24 Research-Oceans*, 114.
- 25 Baretta-Bekker, J.G., Baretta, J.W., Ebenhoh, W., 1997. Microbial dynamics in the
26 marine ecosystem model ERSEM II with decoupled carbon assimilation and nutrient
27 uptake. *J Sea Res*, 38, 195-212.
- 28 Baretta, J.W., Ebenhoh, W., Ruardij, P., 1995. The European Regional Seas
29 Ecosystem Model, a complex marine ecosystem model. *Netherlands Journal of Sea
30 Research*, 33, 233-246.
- 31 Barnier, B., Madec, G., Penduff, T., al., e., 2006. Impact of partial steps and
32 momentum advection schemes in a global ocean circulation model at eddy-permitting
33 resolution. *Ocean Dynamics*, 56, 543-567.
- 34 Baumert, H., Simpson, J., Sundermann, J., 2005. , 2005. *Marine Turbulence –
35 Theories, Observations and Models: The CARTUM Project*. Cambridge,: Cambridge
36 University Press,.
- 37 Beaugrand, G., 2009. Decadal changes in climate and ecosystems in the North
38 Atlantic Ocean and adjacent seas. *Deep Sea Research Part II: Topical Studies in
39 Oceanography*, 56, 656-673.
- 40 Beaugrand, G., Brander K.M., Lindley J.A., Souissi S., P.C., R., 2003a. Plankton
41 effect on cod recruitment in the North Sea. *Nature*, 426, 661-664.
- 42 Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C., 2003b. Plankton
43 effect on cod recruitment in the North Sea. *Nature*, 426, 661-664.

- 1 Beckers, J.-M., Burchard, H., Deleersnijder, E., Mathieu, P.P., 2000. Numerical
2 Discretization of Rotated Diffusion Operators in Ocean Models. *Monthly Weather*
3 *Review*, 12, 2711-2733.
- 4 Billen, G., Lancelot, C., 1988. Modelling benthic nitrogen cycling in temperate
5 coastal ecosystems. . In T.H. Blackburn, J. Sorensen (Eds.), *Nitrogen cycling in*
6 *coastal marine environments*.SCOPE (pp. 341-378.). Chichester: Wiley.
- 7 Blackford, J.C., 1997. An analysis of benthic biological dynamics in a North Sea
8 ecosystem model. *Journal of Sea Research*, 38, 213-230.
- 9 Blackford, J.C., Allen, J.I., Gilbert, F.J., 2004. Ecosystem dynamics at six contrasting
10 sites: a generic model study. *Journal of Marine Systems*, 52, 191-215.
- 11 Branstator, G., Teng, H.Y., 2012. Potential impact of initialization on decadal
12 predictions as assessed for CMIP5 models. *Geophysical Research Letters*, 39.
- 13 Brasseur, P., Gruber, N., Barciela, R., Brander, K., Doron, M., El Moussaoui, A.,
14 Hobday, A.J., Huret, M., Kremeur, A.S., Lehodey, P., Matear, R., Moulin, C.,
15 Murtugudde, R., Senina, I., Svendsen, E., 2009. Integrating Biogeochemistry and
16 Ecology Into Ocean Data Assimilation Systems. *Oceanography*, 22, 206-215.
- 17 Brewin, R.J.W., Lavender, S.J., Hardman-Mountford, N.J., Hirata, T., 2010a. A
18 spectral response approach for detecting dominant phytoplankton size class from
19 satellite remote sensing. *Acta Oceanologica Sinica*, 29, 14-32.
- 20 Brewin, R.J.W., Sathyendranath, S., Hirata, T., Lavender, S.J., Barciela, R.M.,
21 Hardman-Mountford, N.J., 2010b. A three-component model of phytoplankton size
22 class for the Atlantic Ocean. *Ecological Modelling*, 221, 1472-1483.
- 23 Brodeau, L., Barnier, B., Treguier, A.-M., Penduff, T., Gulev, S., 2010. An ERA40-
24 based atmospheric forcing for global ocean circulation models. *Ocean Modelling*, 31,
25 88-104.
- 26 Broerse, A.T.C., Ziveri, P.b., van Hinte, J.E., Honjo, S., 2000. Coccolithophore export
27 production, species composition, and coccolith - CaCO₃ fluxes in the NE Atlantic
28 (34° N 21° W and 48° N 21° W). *Deep Sea Res., Part II*, 47, 1877-1905.
- 29 Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. TOWARD
30 A METABOLIC THEORY OF ECOLOGY. *Ecology*, 85, 1771-1789.
- 31 Bryan, F.O., Hecht, M.W., Smith, R.D., 2007. Resolution convergence and sensitivity
32 studies with North Atlantic circulation models. Part I: The western boundary current
33 system. *Ocean Modelling*, 16, 141-159.
- 34 Bryan, F.O., Smith, R.D., 1998. Modelling the North Atlantic circulation: From eddy-
35 permitting to eddy resolving. *International WOCE Newsletter*, 33, 12-14.
- 36 Bryant, A.D., Heath, M., Gurney, W.S.G., Beare, D.J., Robertson, W., 1997. The
37 seasonal dynamics of *Calanus finmarchicus*: development of a three-dimensional
38 structured population model and application to the northern North Sea. . *J. Sea Res.*,
39 38, 361-379.
- 40 Burchard, H., Rennau, H., 2008. Comparative quantification of physically and
41 numerically induced mixing in ocean models. *Ocean Modelling*, 20, 293-311.

- 1 Burkill, P.H., Mantoura, R.F.C., Llewellyn, C.A., Owens, N.J.P., 1987.
2 Microzooplankton grazing and selectivity of phytoplankton in coastal waters. *Marine*
3 *Biology*, 93, 581-590.
- 4 Canuto, V.M., Howard, A., Cheng, Y., Dubovikov, M.S., 2001. Ocean turbulence.
5 Part I: One-point closure model - Momentum and heat vertical diffusivities. *Journal*
6 *of Physical Oceanography*, 31, 1413-1426.
- 7 Carlotti, F., Poggiale, J.C., 2010. Towards methodological approaches to implement
8 the zooplankton component in "end to end" food-web models. *Prog. Oceanogr.*, 84,
9 20-38.
- 10 Carlotti, F., Radach, G., 1996. Seasonal dynamics of phytoplankton and *Calanus*
11 *finmarchicus* in the North Sea as revealed by a couple one-dimensional model. .
12 *Limnol. Oceanogr.*, 41, 522-539.
- 13 Carlotti, F., Wolf, K.U., 1998. A Lagrangian ensemble model of *Calanus*
14 *finmarchicus* coupled with a 1-D ecosystem model. *Fisheries Oceanography*, 7, 191-
15 204.
- 16 Carlson, C.A., Hansell, D.A., Nelson, N.B., Siegel, D.A., Smethie, W.M., Khatilawa,
17 S., Meyers, M.M., Halewood, E., 2010. Dissolved organic carbon export and
18 subsequent remineralization in the mesopelagic and bathypelagic realms of the North
19 Atlantic basin. . *Deep-Sea Res II*, 57, 1433-1445.
- 20 Carr, M.-E., Friedrichs, M.A.M., Schmeltz, M., Aita, M.N., Antoine, D., Arrigo, k.R.,
21 Asanuma, I., Aumont, O., Barber, R., Behrenfeld, M., Bidigare, R., Buitenhuis, E.T.,
22 Campbell, J., Ciotti, A., Dierssen, H., Dowell, M., Dunne, J., Esaias, W., Gentili, B.,
23 Gregg, W., Groom, S., Hoepffner, N., Ishizaka, J., Kameda, T., Le Quéré, C., Lohrenz,
24 S., Marra, J., Melin, F., Moore, K., Morel, A., Reddy, T.E., Ryan, J., Scardi, M.,
25 Smyth, T., Turpie, K., Tilston, G., Water, K., Yamanaka, Y., 2006. A comparison of
26 global estimates of marine primary production from ocean color. *Deep Sea Research*
27 *II*, 11, 741-770.
- 28 Casini, M., Lovgren, J., Hjelm, J., Cardinale, M., Molinero, J.C., Kornilovs, G., 2008.
29 Multi-level trophic cascades in a heavily exploited open marine ecosystem.
30 *Proceedings of the Royal Society B-Biological Sciences*, 275, 1793-1801.
- 31 Cassou, C., Minvielle, M., Terray, L., Périhaud, C., 2011. A statistical-dynamical
32 scheme for reconstructing ocean forcing in the Atlantic. Part I : weather regimes as
33 predictors for ocean surface variables. *Clim. Dyn.*, 36, 19-39.
- 34 Chanut, J., Barnier, B., Large, W., Debreu, L., Penduff, T., Molines, J.M., Mathiot, P.,
35 2008. Mesoscale eddies in the Labrador Sea and their contribution to convection and
36 restratification. *Journal Of Physical Oceanography*, 38, 1617-1643.
- 37 Chassignet, E.P., Garraffo, Z.D., 2001. Viscosity parameterization and Gulf Stream
38 separation. In P. Muller, D. Henderson (Eds.), *Proceedings of the 'Aha Hu-liko'a*
39 *Hawaiian Winter Workshop*, (pp. 367-374): U. Hawaii.
- 40 Chassignet, E.P., Marshall, D.P., 2008. Gulf Stream separation in numerical ocean
41 models. *Ocean Modeling in an Eddying Regime*, Vol. 177 (pp. 39-61). Washington,
42 DC: AGU.

- 1 Chaudhuri, A.H., Gangopadhyay, A., Bisagni, J.J., 2011. Contrasting Response of the
2 Eastern and Western North Atlantic Circulation to an Episodic Climate Event.
3 *Journal of Physical Oceanography*, 41, 1630-1638.
- 4 Chen, C.S., Huang, H.S., Beardsley, R.C., Liu, H.D., Xu, Q.C., Cowles, G., 2007. A
5 finite volume numerical approach for coastal ocean circulation studies: Comparisons
6 with finite difference models. *Journal of Geophysical Research-Oceans*, 112.
- 7 Chen, C.T.A., Borges, A.V., 2009. Reconciling opposing views on carbon cycling in
8 the coastal ocean: Continental shelves as sinks and near-shore ecosystems as sources
9 of atmospheric CO₂. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 56,
10 578-590.
- 11 Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Pauly, D.,
12 2009. Projecting global marine biodiversity impacts under climate change scenarios.
13 *Fish and Fisheries*, 10, 235-251.
- 14 Chiswell, S.M., 2011. Annual cycles and spring blooms in phytoplankton: don't
15 abandon Sverdrup completely. *Marine Ecology Progress Series*, 443, 39-50.
- 16 Christian, J.R., Anderson, T.R., 2002. Modeling DOM biogeochemistry. In:
17 Biogeochemistry of marine dissolved organic matter In D.A. Hansell, C.A. Carlson
18 (Eds.) (pp. 717-756): Academic Press.
- 19 Ciannelli, L., Hjermann, D.Ø., Lehodey, P., Ottersen, G., Duffy-Anderson, J.T.,
20 Stenseth, N.C., 2005. Climate forcing, food web structure and community dynamics
21 in pelagic marine ecosystems. In A. Belgrano, U. Scharler, J. Dunne, B. Ulanowicz
22 (Eds.), *In Aquatic Food Webs: an Ecosystem Approach* (pp. 143-169): Oxford
23 University Press.
- 24 Ciavatta, S., Torres, R., Saux-Picart, S., Allen, J.I., 2011. Can ocean color
25 assimilation improve biogeochemical hindcasts in shelf seas? *Journal of Geophysical
26 Research-Oceans*, 116.
- 27 Colella, P., Woodward, P.R., 1984. The Piecewise Parabolic Method (PPM) for Gas-
28 Dynamical Simulations. *Journal of Computational Physics*, 54, 174-201.
- 29 Cury, P.M., Shin, Y.J., Planque, B., Durant, J.M., Fromentin, J.M., Kramer-Schadt, S.,
30 Stenseth, N.C., Travers, M., Grimm, V., 2008. Ecosystem oceanography for global
31 change in fisheries. *Trends in Ecology & Evolution*, 23, 338-346.
- 32 D' Asaro, E.A., 2008. Convection and the seeding of the North Atlantic bloom.
33 *Journal of Marine Systems*, 69, 233-237.
- 34 Daskalov, G.M., Grishin, A.N., Rodionov, S., Mihneva, V., 2007. Trophic cascades
35 triggered by overfishing reveal possible mechanisms of ecosystem regime shifts.
36 *Proceedings of the National Academy of Sciences of the United States of America*,
37 104, 10518-10523.
- 38 de Boyer Montégut, C., Madec, G., Fischer, A.S., Lazar, A., Ludicone, D., 2004.
39 Mixed layer depth over the global ocean: an examination of profile data and a profile-
40 based climatology. *J. Geophys. Res.*, 109, C12003. doi:10.1029/2004JC002378.
- 41 de Young, B., Werner, F., Chai, F., Megrey, B., Monfray, P., 2004. Challenges of
42 modeling ocean basin ecosystems. *Science*, 304, 1463-1466.

- 1 DeAngelis, D.L., Cox, D.C., Coutant, C.C., 1979. Cannibalism and size dispersal in
2 young-of-the-year largemouth bass: experiments and model. *Ecological Modelling*, 8,
3 133-148.
- 4 DeAngelis, D.L., Gross, L.J., (Eds.), 1992. *Individual-based Models and Approaches*
5 *in Ecology*. London: Chapman & Hall.
- 6 Delhez, E., Damm, P., de Goede, E., de Kok, J., Dumas, F., Gerritsen, H., Jones, J.,
7 Ozer, J., Pohlmann, T., Rasch, P., Skogen, M., R, P., 2004. Variability of shelf-seas
8 hydrodynamic models: lessons from the NOMADS 2 project. *Journal of Marine*
9 *Systems*, 45 (1-2), 39-53.
- 10 Dickie, L.M., 1976. PREDATION, YIELD, AND ECOLOGICAL EFFICIENCY IN
11 AQUATIC FOOD CHAINS. *Journal of the Fisheries Research Board of Canada*, 33,
12 313-316.
- 13 Dickson, R.R., Curry, R., Yashayaev, I., 2003. Recent changes in the North Atlantic.
14 *Philosophical Transactions of the Royal Society of London. Series A: Mathematical,*
15 *Physical and Engineering Sciences*, 361, 1917-1934.
- 16 Doney, S.C., 1999. Major challenges confronting marine biogeochemical modelling.
17 *Global Biogeochem. Cy.*, 13, 705-714.
- 18 Ducet, N., Le Traon, P.Y., Reverdin, G., 2000. Global high-resolution mapping of
19 ocean circulation from TOPEX/Poseidon and ERS-1 and-2. *Journal Of Geophysical*
20 *Research-Oceans*, 105, 19477-19498.
- 21 Ducklow, H.W., Carlson, C.A., Bates, N.R., Knap, A.H., Michaels, A.F., 1995.
22 DISSOLVED ORGANIC-CARBON AS A COMPONENT OF THE BIOLOGICAL
23 PUMP IN THE NORTH-ATLANTIC OCEAN. *Philosophical Transactions of the*
24 *Royal Society of London Series B-Biological Sciences*, 348, 161-167.
- 25 Ebenhoh, W., Kohlmeier, C., Radford, P.J., 1995. The Benthic Biological Submodel
26 in the European-Regional-Seas- Ecosystem-Model. *Netherlands Journal of Sea*
27 *Research*, 33, 423-452.
- 28 Eden, C., 2007. Eddy length scales in the North Atlantic Ocean. *Journal of*
29 *Geophysical Research-Oceans*, 112.
- 30 Eden, C., Oschlies, A., 2006. Adiabatic reduction of circulation-related CO₂ air-sea
31 flux biases in a North Atlantic carbon-cycle model. *Global Biogeochemical Cycles*,
32 20.
- 33 Egbert, G.D., bennett, A.F., Foreman, M.G.G., 1994. TOPEX/POSEIDON tides
34 estimated using a global inverse model. *Journal of Geophysical Research*, 99, 24821-
35 24852.
- 36 Eppley, R.W., 1972. TEMPERATURE AND PHYTOPLANKTON GROWTH IN
37 SEA. *Fishery Bulletin*, 70, 1063-1085.
- 38 FAO, 2012. The State of the Worlds Fisheries and Aquaculture. (p. 209pp).
- 39 Fasham, M.J.R., Ducklow, H.W., McKelvie, S.M., 1990. A nitrogen-based model of
40 plankton dynamics in the oceanic mixed layer. *J. Mar. Res.*, 48, 591-639.
- 41 Fasham, M.J.R., Sarmiento, J.L., Slater, R.D., Ducklow, H.W., Williams, R., 1993.
42 ECOSYSTEM BEHAVIOR AT BERMUDA STATION-S AND OCEAN

- 1 WEATHER STATION INDIA - A GENERAL-CIRCULATION MODEL AND
2 OBSERVATIONAL ANALYSIS. *Global Biogeochemical Cycles*, 7, 379-415.
- 3 Feng, Y., Hare, C.E., Leblanc, K., et al., 2009. Effects of increased pCO₂ and
4 temperature on the North Atlantic spring bloom. I. The phytoplankton community and
5 biogeochemical response. *Mar. Ecol. Prog. Ser.*, 388, 13-25.
- 6 Fiksen, Ø., 2000. The adaptive timing of diapause - a search for evolutionarily robust
7 strategies in *Calanus finmarchicus*. *ICES Journal of Marine Science*, 57, 1825-1833.
- 8 Fox-Kemper, B., Ferrari, R., Hallberg, R., 2008. Parameterization of mixed layer
9 eddies. Part I: Theory and diagnosis. *Journal of Physical Oceanography*, 38, 1145-
10 1165.
- 11 Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a
12 formerly cod-dominated ecosystem. *Science*, 308, 1621-1623.
- 13 Frank, K.T., Petrie, B., Shackell, N.L., 2007. The ups and downs of trophic control in
14 continental shelf ecosystems. *Trends in Ecology & Evolution*, 22, 236-242.
- 15 Frank, K.T., Petrie, B., Shackell, N.L., Choi, J.S., 2006. Reconciling differences in
16 trophic control in mid-latitude marine ecosystems. *Ecology Letters*, 9, 1096-1105.
- 17 Franks, P.J.S., Chen, C.S., 1996. Plankton production in tidal fronts: A model of
18 Georges Bank in summer. *Journal of Marine Research*, 54, 631-651.
- 19 Galperin, B., Kantha, L.H., Hassid, S., Rossati, A., 1988. A Quasi-Equilibrium
20 Turbulent Energy Model for Geophysical Flows. *Journal of Atmospheric Science*, 45,
21 55-62.
- 22 Garrison, L.P., Link, J.S., 2000. Dietary guild structure of the fish community in the
23 Northeast United States continental shelf ecosystem. *Marine Ecology Progress Series*,
24 202, 231-240.
- 25 Gent, P.R., McWilliams, J.C., 1990. Isopycnal mixing in ocean circulation models.
26 *Journal of Physical Oceanography*, 20, 150-155.
- 27 Gent, P.R., Willebrand, T., McDougall, T., McWilliams, J.L., 1995. Parameterizing
28 eddy-induced tracer transports in ocean circulation models. *Journal of Physical*
29 *Oceanography*, 25, 463-474.
- 30 Gentleman, W., Leising, A., Frost, B., Strom, S., Murray, J., 2003. Functional
31 responses for zooplankton feeding on multiple resources: a review of assumptions and
32 biological dynamics. *Deep-Sea Research II*, 50, 2847-2875.
- 33 Goldberg, S.J., Carlson, C.A., Bock, B., Nelson, N.B., Siegel, D.A., 2010. Meridional
34 variability in dissolved organic matter stocks and diagenetic state within the euphotic
35 and mesopelagic zone of the North Atlantic subtropical gyre. *Mar. Chem.*, 119, 9-21.
- 36 Gordon, J.D., Boudreau, P.R., Mann, K.H., ONG, J.-E., Silvert, W.L., Smith, S.V.,
37 Wattayakorn, G., Wulff, F., Yanagi, T., 1996. LOICZ Biogeochemical modelling
38 guidelines., *LOICZ Reports and Studies No. 5*.
- 39 Gregg, W.W., Casey, N.W., 2007. Modeling Coccolithophores in the global oceans.
40 *Deep-Sea Res. Part II*, 54, 447-477.

- 1 Griffiths, R.W., Linden, P.F., 1982. Laboratory experiments on fronts Part I: Density
2 Driven Boundary Currents. *Geophysical and Astrophysical Fluid Dynamics*, 19, 159-
3 187.
- 4 Grimm, V., Railsback, S.F., 2005. *Individual-based modeling and ecology*. Princeton:
5 Princeton University Press.
- 6 Grossmann, I., Klotzbach, P.J., 2009. A review of North Atlantic modes of natural
7 variability and their driving mechanisms. *Journal of Geophysical Research-*
8 *Atmospheres*, 114.
- 9 Gruber, N., Lachkar, Z., Frenzel, H., Marchesiello, P., Munnich, M., McWilliams,
10 J.C., Nagai, T., Plattner, G.K., 2011. Eddy-induced reduction of biological production
11 in eastern boundary upwelling systems. *Nature Geoscience*, 4, 787-792.
- 12 Handegard, N.O., du Buisson, L., Brehmer, P., Chalmers, S.J., Robertis, A.D., Huse,
13 G., Kloser, R., Macaulay, G., Maury, O., Ressler, P.H., Stenseth, N.C., Godo, O.R., In
14 Press. Towards an acoustic-based coupled observation and modelling system for
15 monitoring and predicting ecosystem dynamics of the open ocean. *Fish and Fisheries*.
- 16 Hansen, R.B., Ducklow H.W., Field, J.G., 1999. *The changing ocean carbon cycle, a*
17 *midterm synthesis of Joint Global Ocean Flux Study*.: Cambridge University Press.
- 18 Hardy, A.C., 1924. The herring in relation to its animate environment. Part 1. The
19 food and feeding habits of the herring with special reference to the east coast of
20 England. . *Fisheries Investigation Series II*, 7, 1-53.
- 21 Harlay, J., Borges, A.V., Van Der Zee, C., Delille, B., Godoi, R.H.M., Schiettecatte,
22 L.S., Roevros, N., Aerts, K., Lapernat, P.E., Rebreanu, L., Groom, S., Daro, M.H.,
23 Van Grieken, R., Chou, L., 2010. Biogeochemical study of a coccolithophore bloom
24 in the northern Bay of Biscay (NE Atlantic Ocean) in June 2004. *Progress in*
25 *Oceanography*, 86, 317-336.
- 26 Hawkins, E., Sutton, R., 2009. The potential to narrow uncertainties in regional
27 Climate predictions. *Bulliten of the Americal Meteorological Society*, 90, 1095-1107.
- 28 Heath, M., Robertson, W., Mardaljevic, J., Gurney, W.S.G., 1997. Modelling the
29 population dynamics of Calanus in the Fair Isle Current off northern Scotland.
30 *Journal of Sea Research*, 38, 381-412.
- 31 Heath, M.R., 2005. Changes in the structure and function of the North Sea fish
32 foodweb, 1973-2000, and the impacts of fishing and climate. *ICES Journal of Marine*
33 *Science*, 62, 847-868.
- 34 Hecht, M.W., Hunke, E., Maltrud, M.E., Petersen, M.R., Wingate, B.A., 2008. Lateral
35 mixing in the eddying regime and a new broad-ranging formulation. In M. Hecht, H.
36 Hasumi (Eds.), *Eddy Resolving Ocean Modeling*: American Geophysical Union.
- 37 Hecht, M.W., Smith, R.D., 2008. Toward a physical understanding of the North
38 Atlantic: A review of model studies in an eddying regime. In M.W. M. W. Hecht, H.
39 Hasumi (Eds.), *Ocean Modeling in an Eddying Regime, Geophys. Monogr. Ser.*, Vol.
40 177, 409 PP., 2008: AGU.
- 41 Helaouet, P., Beaugrand, G., 2007. Macroecology of Calanus finmarchicus and C-
42 helgolandicus in the North Atlantic Ocean and adjacent seas. *Marine Ecology*
43 *Progress Series*, 345, 147-165.

- 1 Henson, S.A., Robinson, I., Allen, J.T., Waniek, J.J., 2006. Effect of meteorological
2 conditions on interannual variability in timing and magnitude of the spring bloom in
3 the Irminger Basin, North Atlantic. *Deep-Sea Research Part I-Oceanographic*
4 *Research Papers*, 53, 1601-1615.
- 5 Hernandez-Leon, S., Gomez, M., Pagazaurtundua, M., Portillo-Hahnefeld, A.,
6 Montero, I., Almeida, C., 2001. Vertical distribution of zooplankton in Canary Island
7 waters : implications for export flux. . *Deep-Sea Res. I*, 48, 1071-1092.
- 8 Hessen, D.O., Anderson, T.R., 2008. Excess carbon in aquatic organisms and
9 ecosystems: Physiological, ecological, and evolutionary implications. . *Limnology and*
10 *Oceanography*, 53, 1685-1696.
- 11 Hirata, T., Hardman-Mountford, N.J., Brewin, R.J.W., Aiken, J., Barlow, R., Suzuki,
12 K., Isada, T., Howell, E., Hashioka, T., Noguchi-Aita, M., Yamanaka, Y., 2011.
13 Synoptic relationships between surface Chlorophyll-a and diagnostic pigments
14 specific to phytoplankton functional types. *Biogeosciences*, 8, 311-327.
- 15 Hjøllø, S.S., Huse, G., Skogen, M.D., Melle, W., 2012. Modelling secondary
16 production in the Norwegian Sea with a fully coupled physical/primary
17 production/individual-based Calanus finmarchicus model system. *Marine Biology*
18 *Research*, 8, 508-526.
- 19 Hofmann, E.E., 1988. Plankton dynamics on the outer southeastern U.S. continental
20 shelf. Part III. A coupled physical-biological model. *J. Mar. Res.*, 46, 919-946.
- 21 Holligan, P.M., Fernandez, E., Aiken, J., Balch, W.M., Boyd, P., Burkill, P.H., Finch,
22 M., Groom, S.B., Malin, G., Muller, K., Purdie, D.A., Robinson, C., Trees, C.C.,
23 Turner, S.M., Vanderwal, P., 1993. A BIOGEOCHEMICAL STUDY OF THE
24 COCCOLITHOPHORE, EMILIANA-HUXLEYI, IN THE NORTH-ATLANTIC.
25 *Global Biogeochemical Cycles*, 7, 879-900.
- 26 Holt, J., Butenschon, M., Wakelin, S.L., Artioli, Y., Allen, J.I., 2012a. Oceanic
27 controls on the primary production of the northwest European continental shelf:
28 model experiments under recent past conditions and a potential future scenario.
29 *Biogeosciences*, 9, 97-117.
- 30 Holt, J., Hughes, S., Hopkins, J., Wakelin, S.L., Holliday, N.P., Dye, S., González-
31 Pola, C., Hjøllø, S.S., Mork, K.A., Nolan, G., Proctor, R., Read, J., Shammon, T.,
32 Sherwin, T., Smyth, T., Tattersall, G., Ward, B., Wiltshire, K.H., 2012b. Multi-
33 decadal variability and trends in the temperature of the northwest European
34 continental shelf: A model-data synthesis. *Progress in Oceanography*, 106, 96-117.
- 35 Holt, J., Huthnance, J., Sharples, J., James, I., Maqueda, M.A.M., Willmott, A.J.,
36 Mooers, C.N.K., In Press. Coastal Ocean Circulation Dynamics. In P. Craig, C.
37 Mooers, Norden, N. Huang (Eds.), *Coupled Coastal Wind-Wave-Current Dynamics*:
38 Cambridge University Press.
- 39 Holt, J., Umlauf, L., 2008. Modelling the tidal mixing fronts and seasonal
40 stratification of the Northwest European Continental shelf. *Continental Shelf*
41 *Research*, 28, 887-903.
- 42 Holt, J., Wakelin, S., Huthnance, J., 2009. Down-welling circulation of the northwest
43 European continental shelf: A driving mechanism for the continental shelf carbon
44 pump. *Geophysical Research Letters*, 36, doi:10.1029/2009GL038997.

- 1 Holt, J.T., Allen, J.I., Proctor, R., Gilbert, F., 2005. Error quantification of a high
2 resolution coupled hydrodynamic-ecosystem coastal-ocean model: part 1 model
3 overview and assessment of the hydrodynamics *Journal of Marine Systems*, 57, 167-
4 188.
- 5 Holt, J.T., James, I.D., 2001. An s-coordinate density evolving model of the North
6 West European Continental Shelf. Part 1 Model description and density structure.
7 *Journal of Geophysical Research*, 106(C7), 14015-14034.
- 8 Holt, J.T., Proctor, R., 2008. The seasonal circulation and volume transport on the
9 northwest European continental shelf: a fine-resolution model study. *Journal of*
10 *Geophysical Research*, 113, C06021, doi:06010.01029/02006JC004034.
- 11 Holt, J.T., Proctor, R., Blackford, J.C., Allen, J.I., Ashworth, M., 2004. Advective
12 controls on primary production in the stratified western Irish Sea: an eddy-resolving
13 model study. *Journal of Geophysical Research*, 109, C05024, doi:
14 05010.01029/02003JC001951.
- 15 Hood, R.R., Bates, N.R., Capone, D.G., Olson, D.B., 2001. Modeling the effects of
16 nitrogen fixation on carbon and nitrogen fluxes at BATS. *Deep-Sea Research II*, 48
17 (8-9), 1609-1648.
- 18 Huisman, J., van Oostveen, P., Weissing, F.J., 1999. Critical depth and critical
19 turbulence: Two different mechanisms for the development of phytoplankton blooms.
20 *Limnology and Oceanography*, 44, 1781-1787.
- 21 Huse, G., 1998. *Life history strategies and spatial dynamics of the Barents Sea*
22 *capelin (Mallotus villosus)*. Bergen: University of Bergen.
- 23 Huse, G., 2001. Modelling habitat choice in fish using adapted random walk. *Sarsia*,
24 86, 477-483.
- 25 Huse, G., 2005. Artificial evolution of *Calanus'* life history strategies under different
26 predation levels. *GLOBEC International Newsletter*, Vol. 11 (p. 19).
- 27 Huse, G., Ellingsen, I.H., 2008. Capelin migrations and climate change - a modelling
28 analysis. *Climatic Change*, 87, 177-191.
- 29 Huse, G., Holst, J.C., Utne, K., Nottestad, L., Melle, W., Slotte, A., Ottersen, G.,
30 Fenchel, T., Uiblein, F., 2012. Effects of interactions between fish populations on
31 ecosystem dynamics in the Norwegian Sea - results of the INFERNO project Preface.
32 *Marine Biology Research*, 8, 415-419.
- 33 Huthnance, J.M., 1995. Circulation, exchange and water masses at the ocean margin:
34 the role of physical processes at the shelf edge. *Progress in Oceanography*, 35, 353-
35 431.
- 36 Huthnance, J.M., Holt, J.T., Wakelin, S.L., 2009. Deep ocean exchange with west-
37 European shelf seas. *Ocean science*, 5, 621-634.
- 38 Hydes, D.J., Gowen, R.J., Holliday, N.P., Shammon, T., Mills, D., 2004. External and
39 internal control of winter concentrations of nutrients (N, P and Si) in north-west
40 European shelf seas. *Estuarine Coastal and Shelf Science*, 59, 151-161.
- 41 Irigoien, X., Head, R., Klenke, U., Meyer-Harms, B., Harbour, D., Niehoff, B., Hirche,
42 H.-J., Harris R., 1998. A high frequency time series at Weathership M, Norwegian

- 1 Sea, during the 1997 spring bloom: feeding of adult female *Calanus finmarchicus*.
2 *Marine Ecology Progress Series*, 172, 127-137.
- 3 James, I.D., 2000. A high-performance explicit vertical advection scheme for ocean
4 models: how PPM can beat the CFL condition. *Applied Mathematical Modelling*, 24,
5 1-9.
- 6 Jennings, S., Warr, K.J., Mackinson, S., 2002. Use of size-based production and
7 stable isotope analyses to predict trophic transfer efficiencies and predator-prey body
8 mass ratios in food webs. *Marine Ecology Progress Series*, 240, 11-20.
- 9 Johannessen, J.A., E.Svendsen, S.Sandven, Johannessen, O.M., K.Lygre, 1989.
10 Three-dimensional structure of mesoscale eddies in the Norwegian Coastal Current.
11 *Journal of Physical Oceanography*, 19, 3-19.
- 12 Josey, S.A., Kent, E.C., Taylor, P.K., 2002. Wind Stress Forcing of the Ocean in the
13 SOC Climatology: Comparisons with the NCEP-NCAR, ECMWF, UWM/COADS,
14 and Hellerman and Rosenstein Datasets. *Journal of Physical Oceanography*, 32,
15 1993-2019.
- 16 Kämpf, J., Backhaus, J.O., 1998. Shallow, brine-driven free convection in polar
17 oceans: Nonhydrostatic numerical process studies. *Journal of Geophysical Research*,
18 103, 5577-5593.
- 19 Kearney, K.A., Stock, C., Aydin, K., Sarmiento, J.L., 2012. Coupling planktonic
20 ecosystem and fisheries food web models for a pelagic ecosystem: Description and
21 validation for the subarctic Pacific. *Ecological Modelling*, 237, 43-62.
- 22 Kerr, S.R., 1974. Theory of Size Distribution in Ecological Communities. *Journal of*
23 *the Fisheries Research Board of Canada*, 31, 1859-1862.
- 24 Kim, H.M., Webster, P.J., Curry, J.A., 2012. Evaluation of short-term climate change
25 prediction in multi-model CMIP5 decadal hindcasts. *Geophysical Research Letters*,
26 39.
- 27 Kooijmann, S.A.L.M., 2000. *Dynamic Energy Mass Budgets in Biological Systems*.
28 Cambridge: Cambridge University Press.
- 29 Large, W.G., McWilliams, J.C., Doney, S.C., 1994. Oceanic vertical mixing: A
30 review and a model with a nonlocal boundary layer parameterization. *Reviews of*
31 *Geophysics*, 32, 363-403.
- 32 Le Quere, C., Harrison, S.P., Prentice, I.C., Buitenhuis, E.T., Aumont, O., Bopp, L.,
33 Claustre, H., Da Cunha, L.C., Geider, R., Giraud, X., Klaas, C., Kohfeld, K.E.,
34 Legendre, L., Manizza, M., Platt, T., Rivkin, R.B., Sathyendranath, S., Uitz, J.,
35 Watson, A.J., Wolf-Gladrow, D., 2005. Ecosystem dynamics based on plankton
36 functional types for global ocean biogeochemistry models. *Global Change Biology*,
37 11, 2016-2040.
- 38 Le Quere, C., Takahashi, T., Buitenhuis, E.T., Rodenbeck, C., Sutherland, S.C., 2010.
39 Impact of climate change and variability on the global oceanic sink of CO₂. *Global*
40 *Biogeochemical Cycles*, 24.
- 41 Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K.,
42 Fromentin, J.M., Hare, S.R., Ottersen, G., Perry, R.I., Roy, C., Van der Lingen, C.D.,

- 1 Werner, F., 2006. Climate variability, fish, and fisheries. *Journal of Climate*, 19,
2 5009-5030.
- 3 Lehodey, P., Maury, O., 2010. CLimate Impacts on Oceanic TOP Predators
4 (CLIOTOP): Introduction to the Special Issue of the CLIOTOP International
5 Symposium, La Paz, Mexico, 3-7 December 2007 Preface. *Progress in Oceanography*,
6 86, 1-7.
- 7 Lehodey, P., Murtugudde, R., Senina, I., 2010. Bridging the gap from ocean models
8 to population dynamics of large marine predators: A model of mid-trophic functional
9 groups. *Progress in Oceanography*, 84, 69-84.
- 10 Lehodey, P., Senina, I., Calmettes, B., Hampton, J., S., N., 2012. Modelling the
11 impact of climate change on Pacific skipjack tuna population and fisheries. *Climatic
12 Change*, DOI 10.1007/s10584-10012-10595-10581.
- 13 Lehodey, P., Senina, I., Murtugudde, R., 2008. A spatial ecosystem and populations
14 dynamics model (SEAPODYM) - Modeling of tuna and tuna-like populations.
15 *Progress in Oceanography*, 78, 304-318.
- 16 Levier, B., Theetten, S., Treguier, A.M., 2007. Description of a NATL025 run with
17 open boundaries of the DRAKKAR project. *Laboratoire de Physique des Oceans,
18 UMR6523, CNRS-Ifremer-UBO, Brest, France*.
- 19 Levy, M., Ferrari, R., Franks, P.J.S., Martin, A.P., Riviere, P., 2012. Bringing physics
20 to life at the submesoscale. *Geophysical Research Letters*, 39.
- 21 Lévy, M., Klein, P., Tréguier, A.-M., Iovino, D., Madec, G., Masson, S., Takahashi,
22 K., 2010. Modifications of gyre circulation by sub-mesoscale physics,. *Ocean
23 Modelling*, 34, 1-15.
- 24 Lewis, K., Allen, J.I., Richardson, A., J, Holt, J.T., 2006. Error quantification of a
25 high resolution coupled hydrodynamic-ecosystem coastal-ocean model: part3,
26 Validation with Continuous Plankton Recorder data. *Journal of Marine Systems*, 63,
27 209-224.
- 28 Loder, J.W., Petrie, 1998. The coastal ocean off Northeastern North America: A large
29 scale view. In A.R. Robinson, K.H. Brink (Eds.), *The Global Coastal Ocean: regional
30 studies and syntheses*, Vol. 11 (pp. 105-133): J. Wiley.
- 31 Lomas, M.W., Burke, A.L., Lomas, D.A., Bell, D.W., Shen, C., Dyhrman, S.T.,
32 Ammerman, J.W., 2010. Sargasso Sea phosphorus biogeochemistry: an important role
33 for dissolved organic phosphorus (DOP). *Biogeosciences*, 7, 695-710.
- 34 Lowe, J.A., Howard, T.P., Pardaens, A., Tinker, J., Holt, J., Wakelin, S., Milne, G.,
35 Leake, J., Wolf, J., Horsburgh, K., Reeder, T., Jenkins, G., Ridley, J., Dye, S.,
36 Bradley, S., . 2009. UK Climate Projections science report: Marine and coastal
37 projections. *Chaos*. Met Office Hadley Centre, Exeter, UK. .
- 38 Lozier, M.S., Dave, A.C., Palter, J.B., Gerber, L.M., Barber, R.T., 2011. On the
39 relationship between stratification and primary productivity in the North Atlantic.
40 *Geophysical Research Letters*, 38, L18609
41 18610.11029/12011gl049414.
- 42 Macdonald, A.M., Wunsch, C., 1996. An estimate of global ocean circulation and
43 heat fluxes. *Nature*, 382, 436-439.

- 1 Madec, G., 2008. NEMO reference manual, ocean dynamic component: NEMO-OPA.
2 Note du Pole de modelisation, Institut Pierre Simon Laplace, Technical Report 27,
3 ISSN No, 1288-1619.
- 4 Mahowald, N.M., Baker, A.R., Bergametti, G., Brooks, N., Duce, R.A., Jickells, T.D.,
5 Kubilay, N., Prospero, J.M., Tegen, I., 2005. Atmospheric global dust cycle and iron
6 inputs to the ocean. *Global Biogeochemical Cycles*, 19.
- 7 Maraldi, C., Chanut, J., Levier, B., Reffray, G., Ayoub, N., De Mey, P., Lyard, F.,
8 Cailleau, S., Drévilion, M., A. Fanjul, E.A., Sotillo, M.G., Marsaleix, P., Team, t.M.,
9 2012. NEMO on the shelf: assessment of the Iberia–Biscay–Ireland configuration.
10 *Ocean Sci. Discuss.*, 9, 499-583.
- 11 Maranon, E., Fernandez, A., Mourino-Carballido, B., Martinez-Garcia, S., Teira, E.,
12 Cermeno, P., Choucino, P., Huete-Ortega, M., Fernandez, E., Calvo-Diaz, A., Moran,
13 X.A.G., Bode, A., Moreno-Ostos, E., Varela, M.M., Patey, M.D., Achterberg, E.P.,
14 2010. Degree of oligotrophy controls the response of microbial plankton to Saharan
15 dust. *Limnology and Oceanography*, 55, 2339-2352.
- 16 Martin, P., Lampitt, R.S., Perry, M.J., Sanders, R., Lee, C., D'Arso, E., 2011. Export
17 and mesopelagic particle flux during a North Atlantic spring diatom bloom *Deep-Sea*
18 *Res. I*, 58, 338-349.
- 19 Mather, R.L., Reynolds, S.E., Wolff, G.A., Williams, R.G., Torres-Valdes, S.,
20 Woodward, E.M.S., Landolfi, A., Pan, X., Sanders, R., Achterburg, E.P., 2008.
21 Phosphorus cycling in the North and South Atlantic Ocean subtropical gyres. . *Nature*
22 *Geoscience*, 1, 439-443.
- 23 Maury, O., Faugeras, B., Shin, Y.-J., Poggiale, J.C., Ben Ari, T., Marsac, F., 2007a.
24 Modelling environmental effects on the size-structured energy flow through marine
25 ecosystems. Part 1: the model. *Progress in Oceanography*, 74, 479-499.
- 26 Maury, O., Shin, Y.-J., Faugeras, B., Ben Ari, T., Marsac, F., 2007b. Modelling
27 environmental effects on the size-structured energy flow through marine ecosystems.
28 Part 2: simulations. *Progress in Oceanography*, 74, 500-514.
- 29 McGillicuddy Jr., D.J., Robinson, A.R., Siegel, D.A., Jannasch, H.W., Johnson, R.,
30 Dickey, T.D., McNeil, J., Michaels, A.F., Knap, A.H., 1998. Influence of mesoscale
31 eddies on new production in the Sargasso Sea. *Nature*, 394, 263-265.
- 32 Miller, C.B., Lynch, D.R., Carlotti, F., Gentleman, W., Lewis, C.V.W., 1998.
33 Coupling of an individual-based population dynamic model of *Calanus finmarchicus*
34 to a circulation model for the Georges Bank region. *Fisheries Oceanography*, 7.
- 35 Minvielle, M., Cassou, C., Bourdallé-Badie, T., Terray, L., Najac, J., 2011. A
36 statistical-dynamical scheme for reconstructing ocean forcing in the Atlantic. Part II :
37 methodology, validation and applicaion to high-resolution ocean models. . *Clim. Dyn.*,
38 36, 401-417.
- 39 Moller, E.F., Maar, M., Jonasdottir, S.H., Nielsen, T.G., Tonnesson, K., 2012. The
40 effect of changes in temperature and food on the development of *Calanus*
41 *finmarchicus* and *Calanus helgolandicus* populations. *Limnology and Oceanography*,
42 57, 211-220.
- 43 Mollmann, C., Muller-Karulis, B., Kornilovs, G., St John, M.A., 2008. Effects of
44 climate and overfishing on zooplankton dynamics and ecosystem structure: regime

- 1 shifts, trophic cascade, and feedback loops in a simple ecosystem. *ICES Journal of*
2 *Marine Science*, 65, 302-310.
- 3 Montagnes, D.J.S., Allen, J., Brown, L., Bulit, C., Davidson, R., Fielding, S., Heath,
4 M., Holliday, N.P., Rasmussen, J., Sanders, R., Waniek, J.J., Wilson, D., 2010. Role
5 of ciliates and other microzooplankton in the Irminger Sea (NW Atlantic Ocean).
6 *Marine Ecology Progress Series*, 411, 101-115.
- 7 Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P., Peterson, C.H., 2007.
8 Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*,
9 315, 1846-1850.
- 10 O’Dea, E.J., Arnold, A., Edwards, K.P., Furner, R., Hyder, P., Martin, M.J., Siddorn,
11 J.R., Storkey, D., While, J., Holt, J.T., Liu, H., 2012. An operational ocean forecast
12 system incorporating NEMO and SST data assimilation for the tidally driven
13 European North-West shelf. *Journal of Operational Oceanography*, 5(1), 3-17.
- 14 Ohman, M.D., Eiane, K., Durbin, E.G., Runge, J.A., Hirche, H.-J., 2004. A
15 comparative study of *Calanus finmarchicus* mortality patterns at five localities in the
16 North Atlantic *ICES Journal of Marine Science*, 61, 687-697.
- 17 Oschlies, A., Garçon, V., 2000. Eddy-induced enhancement of primary production in
18 a model of the North Atlantic Ocean. *Nature*, 394, 266-269.
- 19 Oschlies, A., Koeve, W., Garçon, V., 2000. An eddy-permitting coupled physical-
20 biological model of the North Atlantic 2. Ecosystem dynamics and comparison with
21 satellite and JGOFS local studies data. *Global Biogeochemical Cycles*, 14, 499-523.
- 22 Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades revealed
23 in diverse ecosystems. *Trends in Ecology & Evolution*, 14, 483-488.
- 24 Parsons, T.R., Lalli, C.M., 1988. Comparative oceanic ecology of the plankton
25 communities of the subarctic Atlantic and Pacific oceans. *Oceanogr. Mar. Biol. Ann.*
26 *Rev.*, 26, 317-359.
- 27 Pauly, D., Christensen, V., 1993. *STRATIFIED MODELS OF LARGE MARINE*
28 *ECOSYSTEMS - A GENERAL-APPROACH AND AN APPLICATION TO THE*
29 *SOUTH CHINA SEA*.
- 30 Peliz, A., Rosa, T.L., Santos, M.P., Pissarra, J.L., 2002. Fronts, jets, and counter-
31 flows in the western Iberian upwelling system. *Journal of Marine Systems*, 35, 61-77.
- 32 Pérez, F.F., Castro, C.G., Ríos, A.F., Fraga, F., 2005. Chemical properties of the deep
33 winter mixed layer in the Northeast Atlantic (40-47°N). *Journal of Marine Systems*,
34 54, 115-125.
- 35 Perruche, C., Rivière, P., Lapeyre, G., Carton, X., Pondaven, P., 2011. Effects of
36 surface quasi-geostrophic turbulence on phytoplankton competition and coexistence. *J.*
37 *Mar. Res.*, 69, 105-135.
- 38 Petitgas, P., Rijnsdorp, A.D., Dickey-Collas, M., Engelhard, G.H., Peck, M.A.,
39 Pinnegar, J.K., Drinkwater, K., Huret, M., Nash, R.D.M., 2013. Impacts of climate
40 change on the complex life cycles of fish. *Fisheries Oceanography*, 22, 121-139.
- 41 Pingree, R.D., Sinha, B., Griffiths, C.R., 1999. Seasonality of the European slope
42 current (Goban Spur) and ocean margin exchange. *Continental Shelf Research*, 19,
43 929-975.

- 1 Polimene, L., Allen, J.I., Zavatarelli, M., 2006. Model of interactions between
2 dissolved organic carbon and bacteria in marine systems. *Aquatic Microbial Ecology*,
3 43, 127-138.
- 4 Polvani, L.M., McWilliams, J.C., Spall, M.A., Ford, R., 1994. The coherent structures
5 of shallow-water turbulence: deformation-radius effects, cyclone/anticyclone
6 asymmetry and gravity-wave generation. *Chaos*, 4, 177-186.
- 7 Popova, E.E., Coward, A.C., Nurser, G.A., de Cuevas, B., Fasham, M.J.R., Anderson,
8 T.R., 2006. Mechanisms controlling primary and new production in a global
9 ecosystem model – Part I: Validation of the biological simulation. *Ocean Sci.*,
10 2, 249-266.
- 11 Prather, M.J., 1986. Numerical advection by conservation of 2nd-order moments.
12 *Journal of Geophysical Research-Atmospheres*, 91, 6671-6681.
- 13 Proctor, R., Holt, J.T., Allen, J.I., Blackford, J.C., 2003. Nutrient fluxes and budgets
14 for the North West European Shelf from a three-dimensional model. *Science of the*
15 *Total Environment*, 314-316, 769-785.
- 16 Reid, P.C., Battle, E.J.V., Batten, S.D., Brander, K.M., 2000. Impacts of fisheries on
17 plankton community structure. *ICES Journal of Marine Science*, 57, 495-502.
- 18 Reynolds, R.W., Liu, C., Smith, T.M., Chelton, D.B., Schlax, M.G., Casey, K.S.,
19 2007. Daily High-Resolution-Blended Analyses for Sea Surface Temperature.,
20 *Journal of Climate*, 20(22), 5473-5496.
- 21 Riley, G.A., 1952. Biological oceanography. *Survey of Biological Progress*, 2, 79-104.
- 22 Rippeth, T.P., Wiles, P., Palmer, M.R., Sharples, J., Tweddle, J., 2009. The diapycnal
23 nutrient flux and shear-induced diapycnal mixing in the seasonally stratified western
24 Irish Sea. *Continental Shelf Research*, 29, 1580-1587.
- 25 Rose, K.A., Allen, J.I., Artioli, Y., Barange, M., Blackford, J., Carlotti, F., Cropp, R.,
26 Daewel, U., Edwards, K., Flynn, K., Hill, S.L., HilleRisLambers, R., Huse, G.,
27 Mackinson, S., Megrey, B., Moll, A., Rivkin, R., Salihoglu, B., Schrum, C., Shannon,
28 L., Shin, Y.J., Smith, S.L., Smith, C., Solidoro, C., St John, M., Zhou, M., 2010. End-
29 To-End Models for the Analysis of Marine Ecosystems: Challenges, Issues, and Next
30 Steps. *Marine and Coastal Fisheries*, 2, 115-130.
- 31 Ruardij, P., Vanraaphorst, W., 1995. BENTHIC NUTRIENT REGENERATION IN
32 THE ERSEM ECOSYSTEM MODEL OF THE NORTH-SEA. *Netherlands Journal*
33 *of Sea Research*, 33, 453-483.
- 34 Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L., Wanninkhof,
35 R., Wong, C.S., Wallace, D.W.R., Tilbrook, B., Millero, F.J., Peng, T.-H., Kozyr, A.,
36 Ono, T., Rios, A.F., 2004. The Oceanic Sink for Anthropogenic CO₂. *Science*, 305,
37 367-371.
- 38 Salihoglu, B., Garcon, V., Oschlies, A., Lomas, M.W., 2008. Influence of nutrient
39 utilization and remineralization stoichiometry on phytoplankton species and carbon
40 export: A modeling study at BATS. *Deep-Sea Research Part I-Oceanographic*
41 *Research Papers*, 55, 73-107.

- 1 Sanders, R., Henson, S., Koski, M., De La Rocha, C.L., Painter, S.C., Poulton, A.,
2 Riley, J., Salihoglu, B., Visser, A., Yool, A., Bellerby, R., Martin, A., This volume.
3 The Biological Carbon Pump in the North Atlantic. *Progress in Oceanography*.
- 4 Sarmiento, J.L., Slater, R.D., Fasham, M.J.R., Ducklow, H.W., Toggweiler, J.R.,
5 Evans, G.T., 1993. A seasonal three-dimensional ecosystem model of nitrogen
6 cycling in the North Atlantic euphotic zone. *Global Biogeochem. Cycles*, 7, 417-450.
- 7 Schiebel, R., Brupbacher, U., Schmidtko, S., Nausch, G., Waniek, J., J., Thierstein,
8 H.-R., 2011. Spring coccolithophore production and dispersion in the temperate
9 eastern North Atlantic Ocean. *J. Geophys. Res.*, 116, C08030.
- 10 Schrum, C., Alekseeva, I., St. John, M., 2006. Development of a coupled physical–
11 biological ecosystem model ECOSMO: Part I: Model description and validation for
12 the North Sea. *Journal of Marine Systems*, 61, 79-99.
- 13 Schuster, U., Watson, A.J., 2007. A variable and decreasing sink for atmospheric CO₂
14 in the North Atlantic. *Journal of Geophysical Research-Oceans*, 112.
- 15 Senina, I., Sibert, J., Lehodey, P., 2008. Parameter estimation for basin-scale
16 ecosystem-linked population models of large pelagic predators: Application to
17 skipjack tuna. *Progress in Oceanography*, 78, 319-335.
- 18 Sharples, J., Moore, C.M., Rippeth, T.P., Holligan, P.M., Hydes, D.J., Fisher, N.R.,
19 Simpson, J.H., 2001. Phytoplankton distribution and survival in the thermocline.
20 *Limnology and Oceanography*, 46(3), 486-496.
- 21 Shchepetkin, A.F., McWilliams, J.C., 2003. A method for computing horizontal
22 pressure-gradient force in an oceanic model with a nonaligned vertical coordinate.
23 *Journal of Geophysical Research-Oceans*, 108.
- 24 Sherwin, T.J., Williams, M.O., Turrell, W.R., Hughes, S.L., Miller, P.I., 2006. A
25 description and analysis of mesoscale variability in the Faroe-Shetland Channel.
26 *Journal of Geophysical Research-Oceans*, 111.
- 27 Shutler, J.D., Land, P.E., Brown, C.W., Findlay, H.S., Donlon, C.J., Medland, M.,
28 Snooke, R., Blackford, J.C., 2012. Coccolithophore surface distributions in the North
29 Atlantic and their modulation of the air-sea flux of CO₂ from 10 years of satellite
30 Earth observation data. *Biogeosciences Discussions*, 9, 5823-5848.
- 31 Sibert, J., Senina, I., Lehodey, P., Hampton, J., 2012. Shifting from marine reserves to
32 maritime zoning for conservation of Pacific bigeye tuna (*Thunnus obesus*).
33 *Proceedings of the National Academy of Sciences*, 109(44), 18221-18225.
- 34 Simmons, H.L., Jayne, S.R., St Laurent, L.C., Weaver, A.J., 2004. Tidally driven
35 mixing in a numerical model of the ocean general circulation. *Ocean Modelling*, 6,
36 245-263.
- 37 Simpson, J.H., Hunter, J.R., 1974. Fronts in the Irish Sea. *Nature*, 250, 404-406.
- 38 Sinha, B., Buitenhuis, E.T., Quere, C.L., Anderson, T.R., 2010. Comparison of the
39 emergent behavior of a complex ecosystem model in two ocean general circulation
40 models. *Progress in Oceanography*, 84, 204-224.
- 41 Skogen, M.D., Budgell, W.P., Rey, F., 2007. Interannual variability in Nordic seas
42 primary production. *ICES Journal of Marine Science*, 64, 889-898.

- 1 Skogen, M.D., Drinkwater, K., Hjollo, S.S., Schrum, C., 2011. North Sea sensitivity
2 to atmospheric forcing. *Journal of Marine Systems*, 85, 106-114.
- 3 Skogen, M.D., Svendsen, E., Berntsen, J., Aksnes, D., Ulvestad, K.B., 1995.
4 Modelling the Primary Production in the North Sea using a Coupled Three-
5 dimensional Physical-Chemical-
6 Biological Ocean Model. *Estuarine, Coastal and Shelf Science.*, 41, 545-565.
- 7 Soulsby, R.L., 1983. The bottom boundary layer of the shelf sea. In B. John (Ed.), *The*
8 *physical oceanography of coastal and shelf seas* (pp. 189-266). New York: Elsevier.
- 9 Souza, A.J., Simpson, J.H., Harikrishnan, M., Malarkey, J., 2001. Flow structure and
10 seasonality in the Hebridean slope current. *Oceanologica ACTA*, 24, S63-S76.
- 11 Spiers, D.C., Gurney, W.S.C., Heath, M.R., Horbelt, W., Wood, S.N., de Cuevas,
12 B.A., 2006. Ocean-scale modelling of the distribution, abundance, and seasonal
13 dynamics of the copepod *Calanus finmarchicus*. *Mar. Ecol. Prog. Ser.*, 313, 173-192.
- 14 Spiers, D.C., Gurney, W.S.C., Heath, M.R., Wood, S.N., 2005. Modelling the basin-
15 scale demography of *Calanus finmarchicus* in the north-east Atlantic. *Fish.*
16 *Oceanogr.*, 14, 333-358.
- 17 Spitz, Y.H., Moisan, J.R., Abbott, M.R., 2001. Configuring an ecosystem model using
18 data from the Bermuda-Atlantic Time Series (BATS). *Deep-Sea Research II*, 48 (8-9),
19 1733-1768.
- 20 Stammer, D., Boning, C., 1996. Generation and distribution of mesoscale eddies in
21 the North Atlantic Ocean. In W. Krauss (Ed.), *The warmwatershpere of the North*
22 *Atlantic Ocean* (pp. 159-193): Gebruder Borntraeger.
- 23 Steele, J.H., 1998. Regime shifts in marine ecosystems. *Ecological Applications*, 8,
24 S33-S36.
- 25 Steele, J.H., Collie, J.S., Bisagni, J.J., Gifford, D.J., Fogarty, M.J., Link, J.S., Sullivan,
26 B.K., Sieracki, M.E., Beet, A.R., Mountain, D.G., Durbin, E.G., Palka, D.,
27 Stockhausen, W.T., 2007. Balancing end-to-end budgets of the Georges Bank
28 ecosystem. *Progress in Oceanography*, 74, 423-448.
- 29 Steele, J.H., Ruzicka, J.J., 2011. Constructing end-to-end models using ECOPATH
30 data. *Journal of Marine Systems*, 87, 227-238.
- 31 Stegert, C., Moll, A., Kreis, M., 2009. Validation of the three-dimensional ECOHAM
32 model in the German Bight for 2004 including population dynamics of *Pseudocalanus*
33 *elongatus*. *J. Sea Res.*, 62, 1-15.
- 34 Steinberg, D.K., Goldthwait, S.A., Hansell, D.A., 2002. Zooplankton vertical
35 migration and the active transport of dissolved organic and inorganic nitrogen in the
36 Sargasso Sea. *Deep-Sea Res. I*, 49, 1445-1461.
- 37 Stock, C.A., Alexander, M.A., Bond, N.A., Brander, K.M., Cheung, W.W.L.,
38 Curchitser, E.N., Delworth, T.L., Dunne, J.P., Griffies, S.M., Haltuch, M.A., Hare,
39 J.A., Hollowed, A.B., Lehodey, P., Levin, S.A., Link, J.S., Rose, K.A., Rykaczewski,
40 R.R., Sarmiento, J.L., Stouffer, R.J., Schwing, F.B., Vecchi, G.A., Werner, F.E., 2011.
41 On the use of IPCC-class models to assess the impact of climate on Living Marine
42 Resources. *Progress in Oceanography*, 88, 1-27.

- 1 Stoecker, D.K., 1998. Conceptual models of mixotrophy in planktonic protists and
2 some ecological and evolutionary implications. *Eur. J. Protistology*, 34, 281-290.
- 3 Sudre, J., Morrow, R., 2008. Global surface currents : a high-resolution product for
4 investigating ocean dynamics. *Ocean Dynamics*, 58, 101-118.
- 5 Sverdrup, H.U., 1953. On Conditions for the Vernal Blooming of Phytoplankton *J.*
6 *Cons. int. Explor. Mer*, 18(3), doi: 10.1093/icesjms/1018.1093.1287.
- 7 Taylor, A.H., Allen, J.I., Clark, P.A., 2002. Extraction of a weak climatic signal by an
8 ecosystem. *Nature*, 416, 629-632.
- 9 Taylor, J.R., Ferrari, R., 2011. Shutdown of turbulent convection as a new criterion
10 for the onset of spring phytoplankton blooms. *Limnology and Oceanography*, 56,
11 2293-2307.
- 12 Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An Overview of CMIP5 and the
13 Experiment Design. *Bulletin of the American meteorological society (BAMS)*,
14 DOI:10.1175/BAMS-D-1111-00094.00091.
- 15 Tett, P., .B., Joint I, R., Purdie, D.A., Baars, M., Oosterhuis, S., Daneri, G., Hannah,
16 F., Mills, D.K., Plummer, D.H., Pomroy, A.J., Walne, A.W., Witte, H.J., 1994.
17 Biological consequences of tidal stirring gradients in the North Sea. In D. Charnock H,
18 H.J. KR, Liss PS, Simpson JH, Tett PB, (Eds.), *Understanding the North Sea System*
19 (pp. 115-130). London: Chapman & Hall.
- 20 Treguier, A.M., Deshayes, J., Lique, C., Dussin, R., Molines, J.M., 2012. Eddy
21 contributions to the meridional transport of salt in the North Atlantic. *Journal of*
22 *Geophysical Research-Oceans*, 117.
- 23 Treguier, A.M., Theetten, S., Chassignet, E.P., Penduff, T., Smith, R., Talley, L.,
24 Beismann, J.O., Boning, C., 2005. The North Atlantic subpolar gyre in four high-
25 resolution models. *Journal Of Physical Oceanography*, 35, 757-774.
- 26 Tseng, Y.H., Ferziger, J.H., 2003. A ghost-cell immersed boundary method for flow
27 in complex geometry. *Journal of Computational Physics*, 192, 593-623.
- 28 Umlauf, L., Burchard, H., 2003. A generic length-scale equation for geophysical
29 turbulence models. *Journal of Marine Research*, 61, 235-265.
- 30 Umlauf, L., Burchard, H., 2005. Second-order turbulence closure models for
31 geophysical boundary layers. A review of recent work. *Continental Shelf Research*,
32 25, 795-827.
- 33 Utne, K.R., Hjøllø, S.S., Huse, G., Skogen, M., 2012. Estimating consumption of
34 *Calanus finmarchicus* by planktivorous fish in the Norwegian Sea estimated
35 from using a fully coupled 3D model system. *Marine Biology Research*, 8, 527-547.
- 36 Utne, K.R., Huse, G., 2012. Estimating the horizontal and temporal overlap of pelagic
37 fish distribution in the Norwegian Sea using individual-based modelling. *Mar. Biol.*
38 *Res.*, 8, 548-567.
- 39 Vallino, J.J., 2000. Improving marine ecosystem models: Use of data assimilation and
40 mesocosm experiments. *Journal of Marine Research*, 58, 117-164.

- 1 Vichi, M., Pinardi, N., Masina, S., 2007. A generalized model of pelagic
2 biogeochemistry for the global ocean ecosystem. Part I: Theory. *Journal of Marine*
3 *Systems*, 64, 89-109.
- 4 Wakelin, S.L., Holt, J.T., Blackford, J.C., Allen, J.I., Butenschon, M., Artioli, Y.,
5 2012. Modelling the carbon fluxes of the Northwest European Continental Shelf:
6 validation and budgets. *Journal of Geophysical Research*, 117, C05020,
7 doi:10.1029/2011JC007402
- 8 Wakelin, S.L., Holt, J.T., Proctor, R., 2009. The influence of initial conditions and
9 open boundary conditions on shelf circulation in a 3D ocean-shelf model of the North
10 East Atlantic. *Ocean Dynamics*, 59, 67-81 DOI: 10.1007/s10236-10008-10164-10233.
- 11 Walsh, J.J., Dieterle, D.A., Meyers, M.B., 1988. A simulation analysis of the fate of
12 phytoplankton within the Mid-Atlantic Bight. *Cont. Shelf Res.*, 8, 757-787.
- 13 Waniek, J.J., 2003. The role of physical forcing in initiation of spring blooms in the
14 northeast Atlantic. *J. Mar. Syst.*, 39, 57-82.
- 15 Ward, B.A., Waniek, J.J., 2007. Phytoplankton growth conditions during autumn and
16 winter in the Irminger Sea, North Atlantic. *Marine Ecology Progress Series*, 334, 47-
17 61.
- 18 Watson, A.J., Schuster, U., Bakker, D.C.E., Bates, N.R., Corbiere, A., Gonzalez-
19 Davila, M., Friedrich, T., Hauck, J., Heinze, C., Johannessen, T., Kortzinger, A.,
20 Metzl, N., Olafsson, J., Olsen, A., Oschlies, A., Padin, X.A., Pfeil, B., Santana-
21 Casiano, J.M., Steinhoff, T., Telszewski, M., Rios, A.F., Wallace, D.W.R.,
22 Wanninkhof, R., 2009. Tracking the Variable North Atlantic Sink for Atmospheric
23 CO₂. *Science*, 326, 1391-1393.
- 24 Wehde, H., Backhaus, J.O., Hegseth, E.N., 2001. The influence of oceanic convection
25 in primary production. *Ecological Modelling* 138, 115-126.
- 26 Wiebe, P.H., Harris, R.P., St. John, M.A., Werner, F.E., de Young, B., 2009., P.P.E.,
27 (Eds.), 2009. *BASIN: Basin-scale Analysis, Synthesis, and INtegration. Science Plan*
28 *and Implementation Strategy.* .
- 29 Willebrand, J., Barnier, B., Boning, C., Dieterich, C., Killworth, P.D., Le Provost, C.,
30 Jia, Y.L., Molines, J.M., New, A.L., 2001. Circulation characteristics in three eddy-
31 permitting models of the North Atlantic. *Progress in Oceanography*, 48, 123-161.
- 32 Wroblewski, J.S., 1977. A model of phytoplankton plume formation during variable
33 Oregon upwelling. *J. Mar. Res.*, 35.
- 34 Wu, J., Sunda, W., Boyle, E.A., Karl, D.M., 2000. Phosphate depletion in the Western
35 Atlantic Ocean. *Science*, 289, 759-762.
- 36 Yool, A., Popova, E.E., Anderson, T.R., 2011. MEDUSA: a new intermediate
37 complexity plankton ecosystem model for the global domain. *Geosci. Model Dev.*, 3,
38 381-417.
- 39 Zubkov, M., GA, T., 1998. High bacterivory by the smallest phytoplankton in the
40 North Atlantic Ocean. *Nature*, 455, 224-226.

41
42

1
23 **Tables**

4 Table 1: List of the EURO-BASIN suite of models and references

Configuration	Physical model	LTL model	HTL model
Global 1/4°	NEMO ¹	MEDUSA ²	
North Atlantic 1/4°	NEMO	ERSEM ³ PISCES ⁴	SEAPODYM-MTL ⁶ IBM ⁷ APECOSM ⁸
Northern North Atlantic 1/12°	NEMO-Shelf ⁵	ERSEM ³	
2D	Convection ⁹	IBM	

5 Model references: ¹(Madec, 2008);²(Yool et al., 2011); ³(Baretta et al., 1995;
6 Blackford et al., 2004); ⁴(Aumont et al., 2003); ⁵(Maraldi et al., 2012; O’Dea et al.,
7 2012);⁶(Lehodey et al., 2008); ⁷(Utne et al., 2012; Utne and Huse, 2012); ⁸(Maury et
8 al., 2007a; Maury et al., 2007b);⁹(Kämpf and Backhaus, 1998)

9 Table 2: Summary of the model runs shown in Figures 8, 9, 10

Model	NEMO configuration	Atmospheric Forcing	References
MEDUSA	1° global	ERA 40	Yool et al 2011
PISCES	½° global	DFS4	Aumont et al, 2003
ERSEM	1° global	ERA 40	Blackford et al 2004

10
11

1 **Figures**

2 **Figure 1** Schematic of **a.** open-ocean and shelf sea carbon pumps. Here shown for a
3 downwelling shelf. In the upwelling case both C and N (nutrients) tend to be
4 transported from the deep ocean to the shelf. **b.** a simplistic representation of the
5 marine ecosystem.

6 **Figure 2** The first baroclinic Rossby Radius (log10 km) from the ORCA083 model.
7 This is calculated using a shooting method from an average annual cycles of monthly
8 mean density values. The maximum value is shown here.

9 **Figure 3** Mean surface current for 2006 in 3 global NEMO simulations: a) 1°, b) 1/4°,
10 c) 1/12° ; d) Observations (CTOH; Sudre and Morrow, 2008)

11 **Figure 4** Mean march 2006 MLD based on a 0.2°C density criterion in 3 global
12 NEMO simulations: a) 1°, b) 1/4°, c) 1/12° ; d) Climatological observations (de Boyer
13 Montégut et al., 2004)

14 **Figure 5** Mean SST for 2006 in 3 global NEMO simulations: a) 1°, b) 1/4°, c) 1/12° ;
15 d) Observations (Reynolds SST; Reynolds et al., 2007)

16 **Figure 6** Upper ocean temperature section at 51°N August: a.) Observation (WOA);
17 b.) 1/12° Global; c.) 1/12° EURO-BASIN Northern North Atlantic Model.

18 **Figure 7** Results from the 2D non-hydrostatic convection IBM model. Top: Profile
19 timeseries of simulated chlorophyll concentration [mg Chl m^{-3}] in 1997 at Station M.
20 Black line indicates the mixed layer depth. Bottom: Chlorophyll concentrations over
21 different integration depth: 100m (red); mixed layer (green). Black dots show field
22 measurements (100m).

23 **Figure 8** Schematics of the three LTL models included in EURO-BASIN: a.)
24 PISCES ;b.) MEDUSA; c.) ERSEM

25 **Figure 9** Meridional transect through the N Atlantic comparing the outputs of
26 SeaWifs (dotted) with the EURO-BASIN models PISCES (green), MEDUSA (red)
27 and ERSEM (blue).

28 **Figure 10** Annual mean sea surface chlorophyll (mg m^{-3}), percentage fraction of
29 diatoms and percentage fraction of non-diatoms (1998-2004), for PISCES (a, b, c),

1 MEDUSA (d, e, f), ERSEM (g, h, i) along with estimates from the SeaWIFS satellite
2 (Hirata et al 2011 j, k l). See Table 2.

3 **Figure 11** Density plots of diatom fraction (%) against \log_{10} chlorophyll for a)
4 PISCES, b) MEDUSA, c) ERSEM and d) SeaWifs.

5 **Figure 12** Mid-trophic functional groups. Top: echogram showing monthly average
6 (Nov 2004) diurnal variation from the stationary lander located at the Mid Atlantic
7 Ridge (MarEco Project; kindly from Nils Olav Handegard, IMR, Norway) with
8 identified MTL groups (m- for migrant, hm- for highly-migrant), according to
9 Lehodey et al (2010). Middle and bottom: comparison between predicted biomass of
10 epipelagic and bathypelagic mid-trophic functional groups at a resolution $1/12^\circ$.

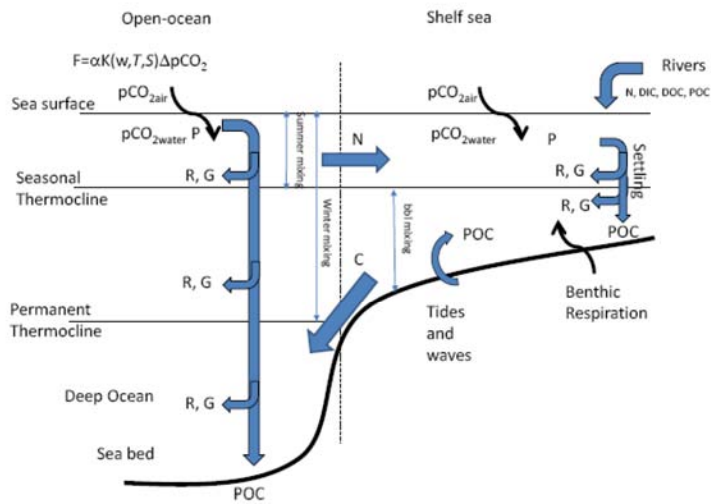
11 **Figure 13** The first SEAPODYM application to North Atlantic Albacore tuna. The
12 maps show an average decadal distribution of albacore larvae (Nb. km^{-2}) and adult
13 (metric t km^{-2}) density during first and last decade of the series, with total catch
14 proportional to circle size superimposed on adult distribution. The bottom plot
15 compares the time series of predicted albacore recruitment from the model
16 SEAPODYM with (black curve) and without (red curve) fishing impact.

17 **Figure 14** Schematic diagram of the relationship between the EURO-BASIN models

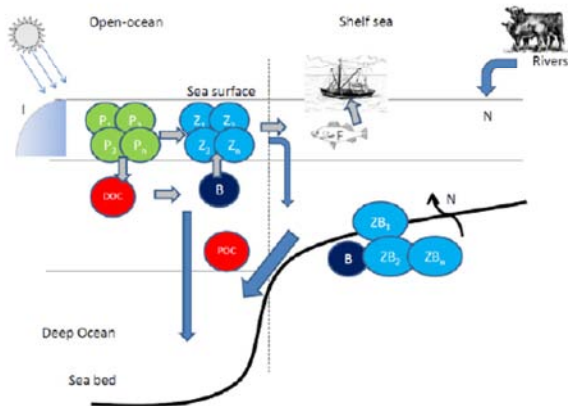
18

1

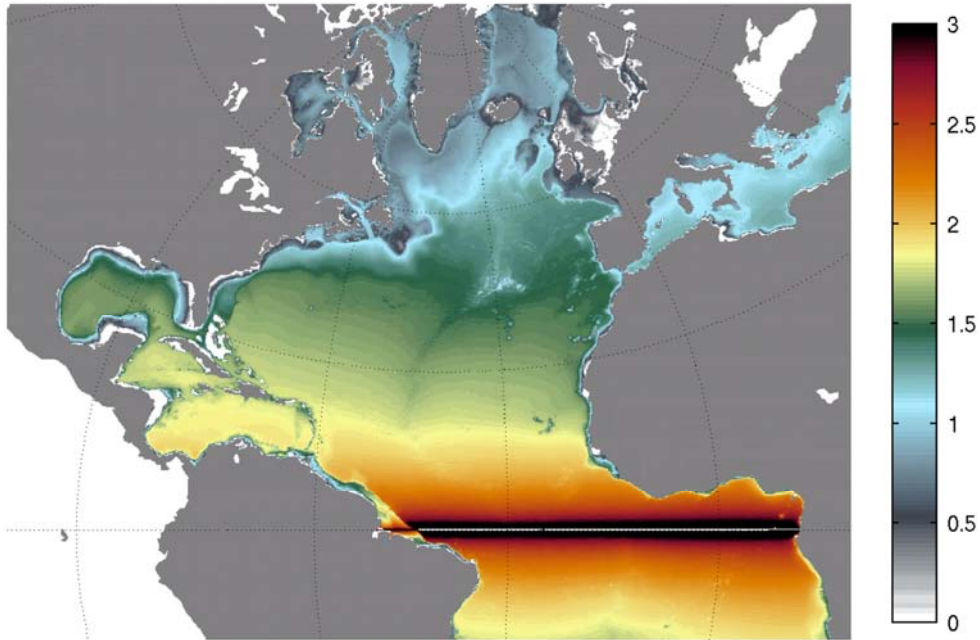
a.



b.



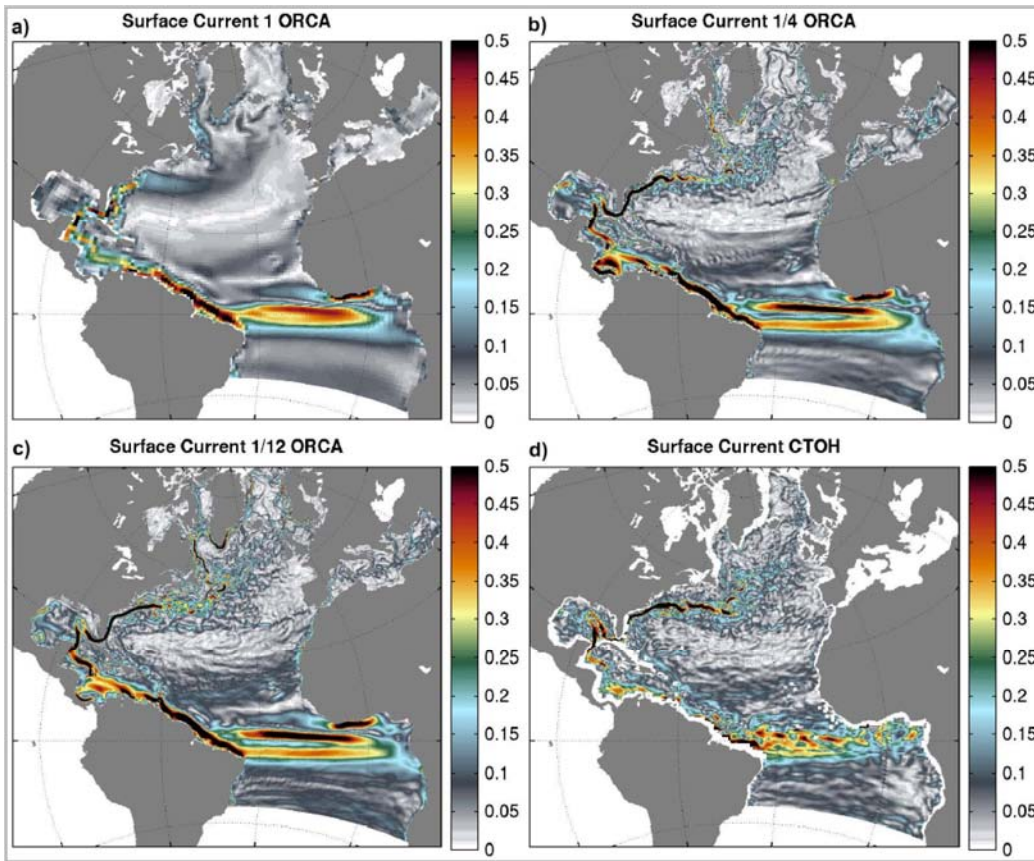
2

Rossby Radius (log₁₀ km)

1

2

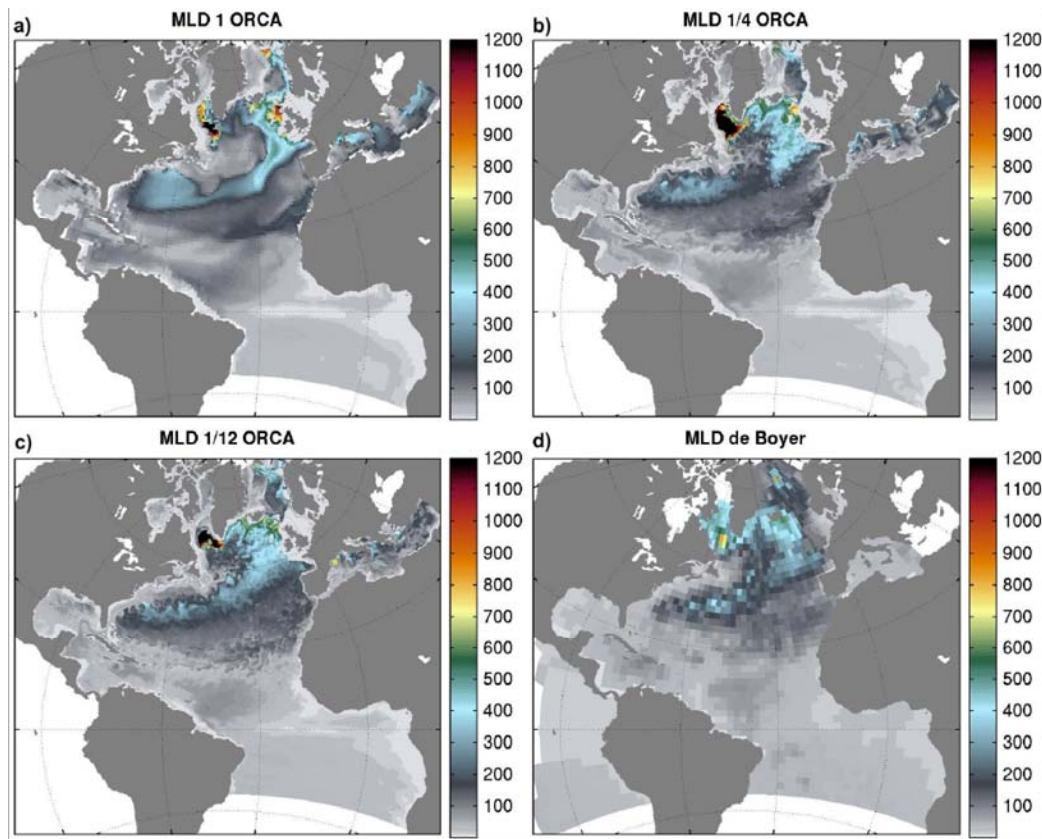
ACCEPTED MANUSCRIPT



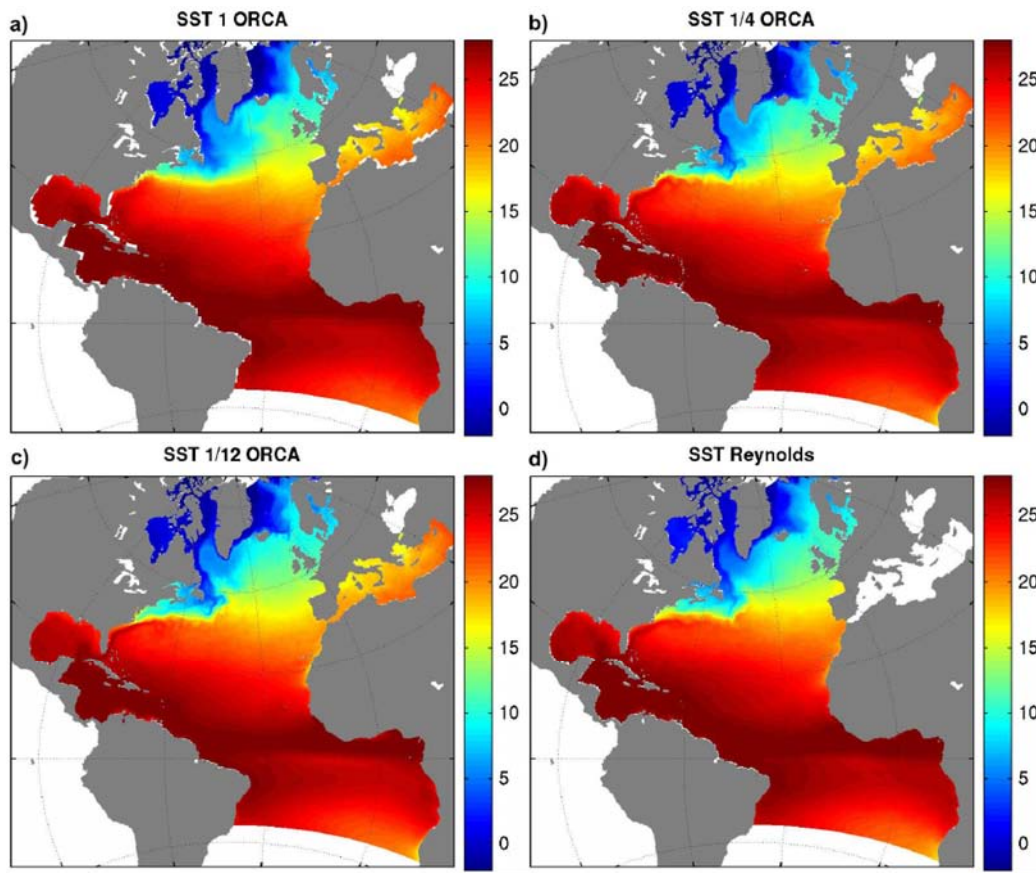
1

2

ACCEPTED

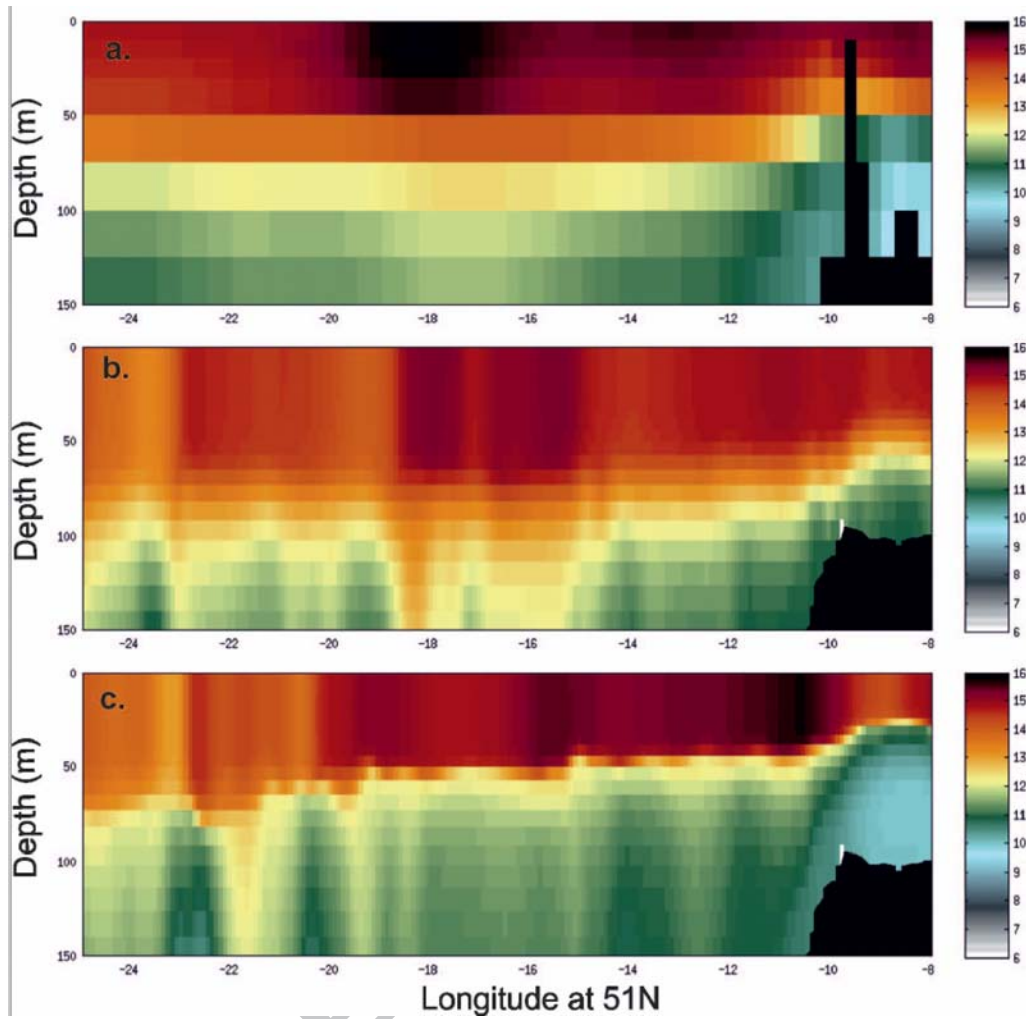


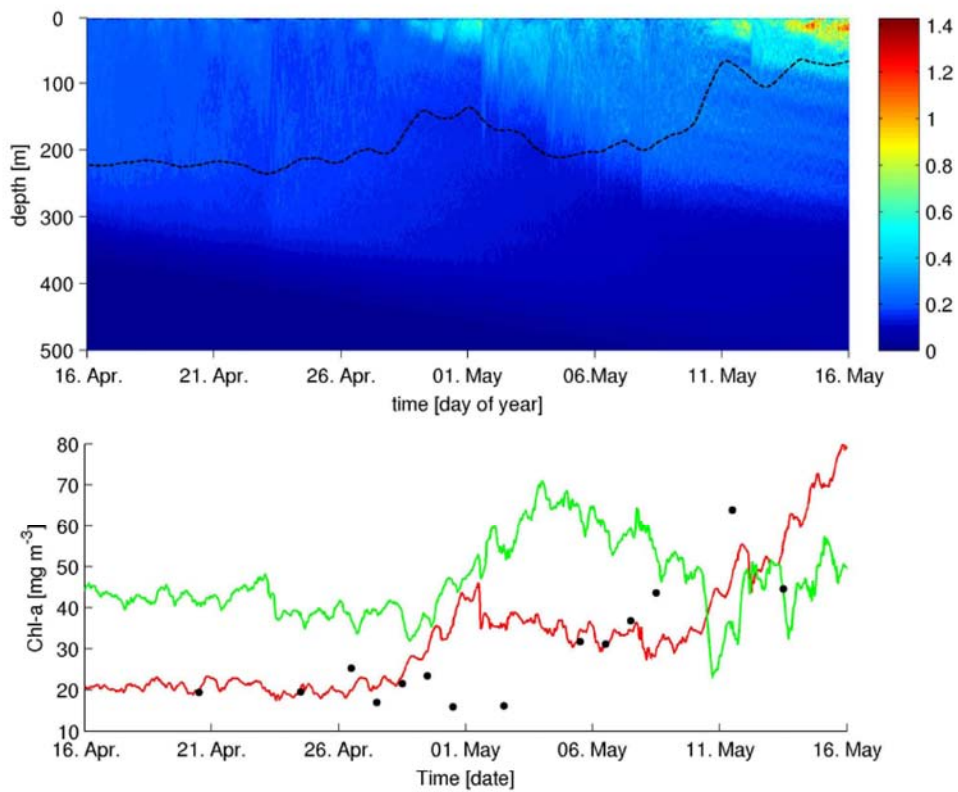
1



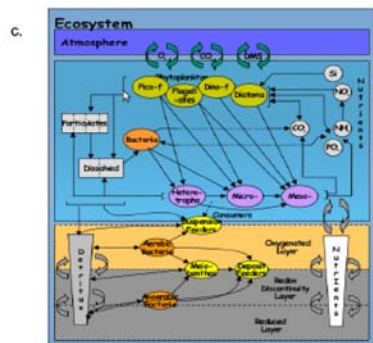
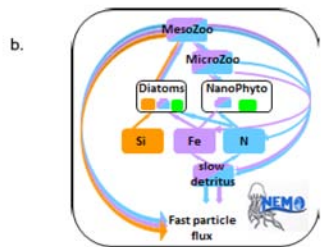
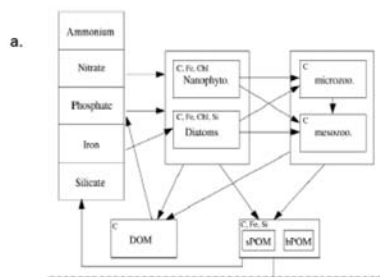
1

ACCEPTED

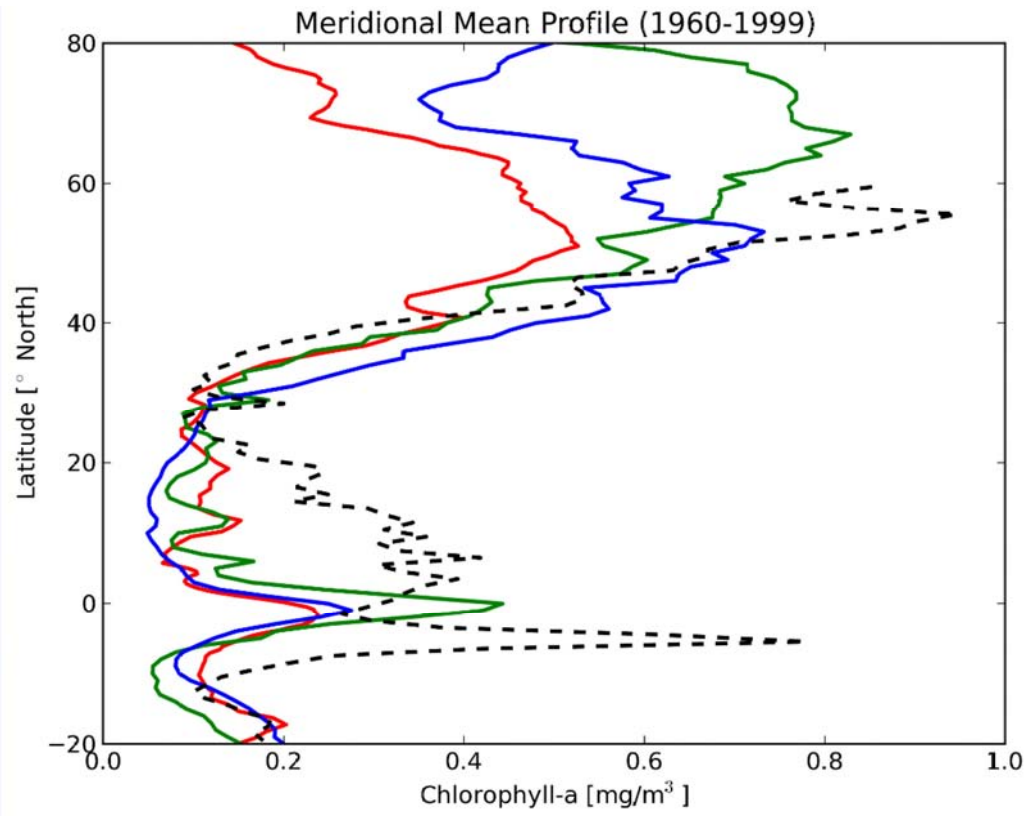




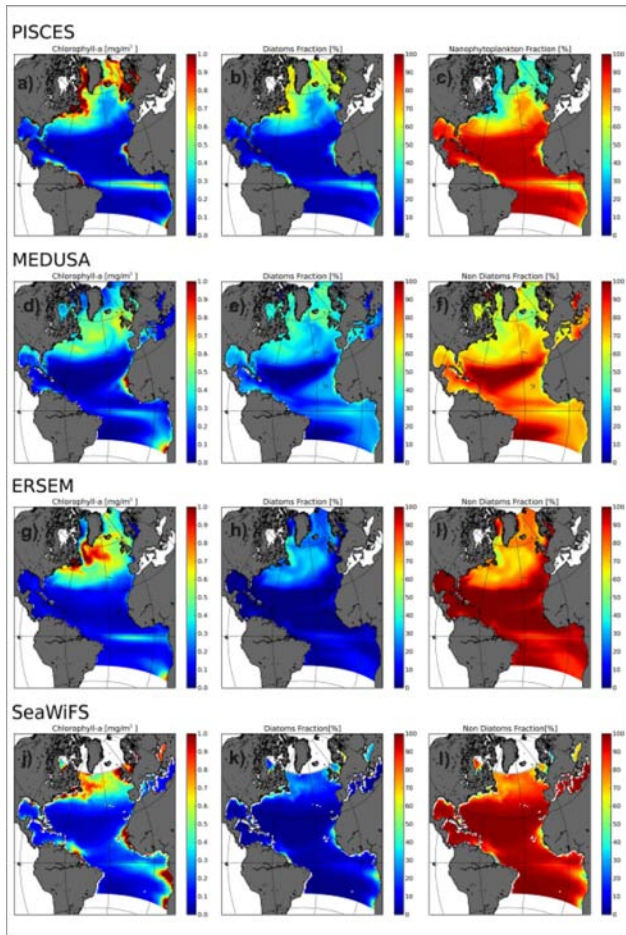
1



1

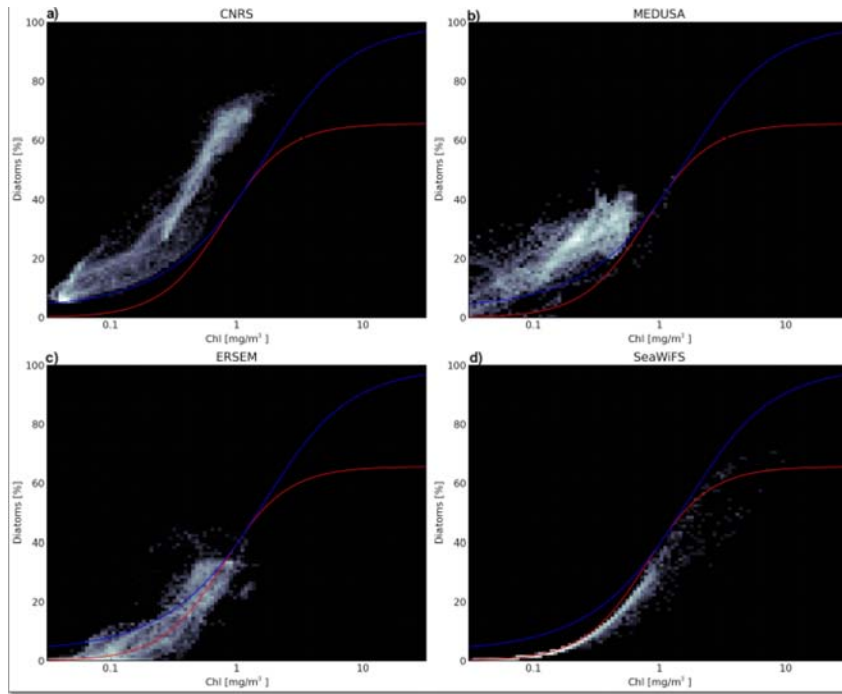


ACCEPTED MANUSCRIPT



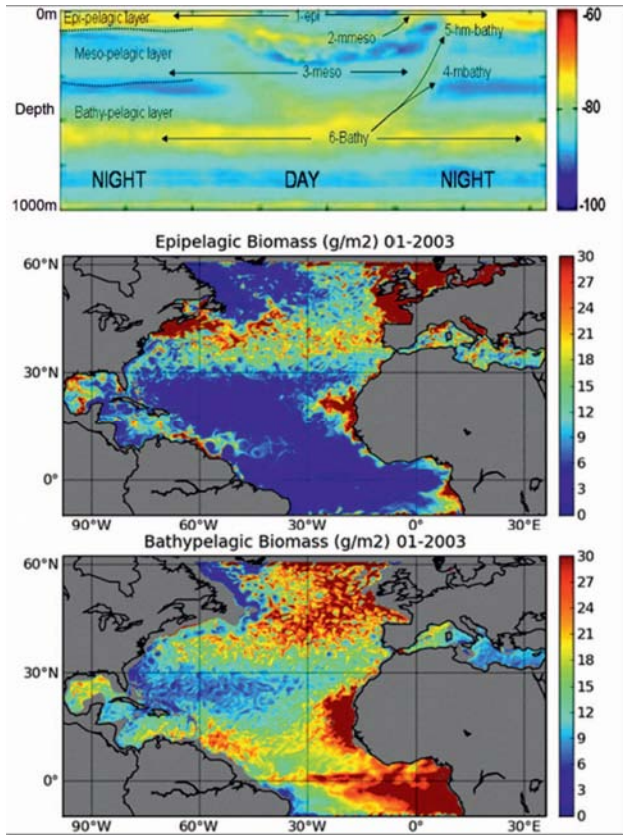
1

2



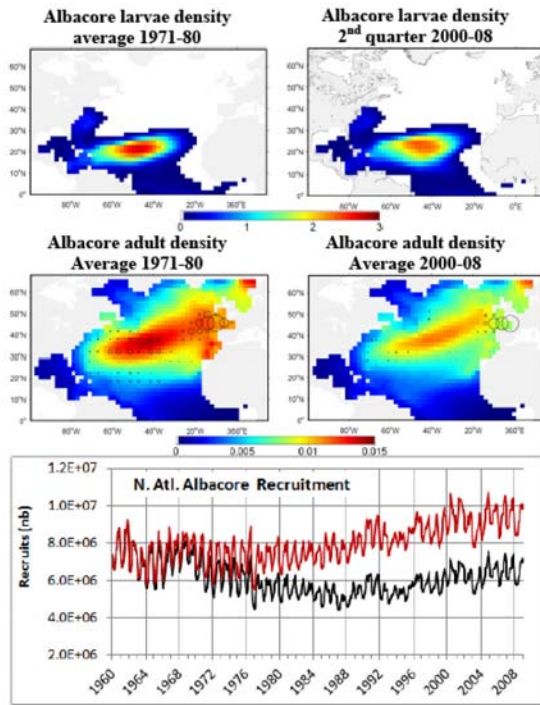
1

2



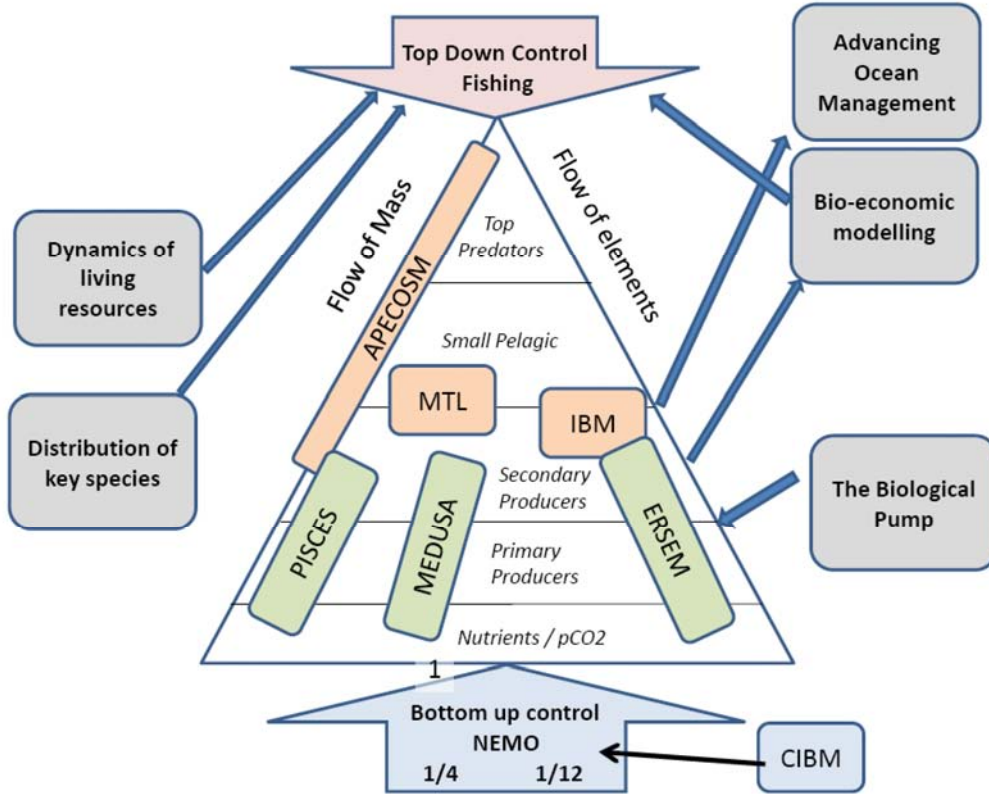
1

2



1

2



1

2

ACCEPTED MANUSCRIPT